Assessing species- and population-level vulnerability to climate-driven phenological mismatch in Pacific salmon

by

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Abstract

Climate change is shifting the timing of life-cycle events, or phenology, of species at different rates, reshuffling species interactions, and sometimes resulting in consumer-resource mismatches, which can impact consumer fitness, survival, and population growth. Indeed, the match/mismatch hypothesis posits that a temporal mismatch between a consumer and its resource during a critical life stage will decrease consumer survival. Migratory species such as Pacific salmon move through multiple environments, experiencing different rates of climate change, and share the migratory challenge of matching with temporally limited resources that shift through time and space. For emigrating juvenile salmon smolts, survival during the critical early marine life stage may depend on matching with peak prey availability upon ocean entrance. Here I examine the vulnerability of Pacific salmon to phenological mismatches during the early marine life stage. In Chapter 2, I use a large-scale synthesis to show unpredictable patterns in phenological change across populations of Pacific salmon, which result in seemingly random rates of phenological mismatch with marine prey. In Chapter 3, I use a unique dataset of individually marked steelhead trout smolts to examine both individual and cohort marine survival across 14 years, demonstrating that size, outmigration timing, and a phenological match between smolts and annual phenology of the cold-water zooplankton community, are important predictors of marine survival. Thus, some species and populations of Pacific salmon are being exposed to phenological mismatches which negatively impact survival. In Chapter 4, using an experimental approach, I develop relationships between body condition and either prolonged swim performance or survival. Finally, in Chapter 5, I found within- and across-population variation in body condition of wild sockeye salmon smolts before and after migration. Using a bioenergetic model and the relationship between Fulton's condition factor and swim performance developed in Chapter 4, I predicted starvation resistance, that is, days to death, to demonstrate how body condition could be used as a proxy for sensitivity to starvation associated with phenological mismatch. Collectively, these studies demonstrate that salmon are resilient to infrequent phenological mismatches, but it is unclear how anthropogenic change will impact vulnerability into the future.

Keywords: Climate change, Match/mismatch hypothesis, Migration, Phenology, Salmon, Sensitivity

Dedication

To my family

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Chapter 1

General Introduction

Climate change is altering the seasonality of temperate regions, resulting in earlier springs and later falls, but it is unclear if the life histories of animals can keep pace with this change. Global surface temperatures have increased on average 0.80°C over the last century, a trend that is expected to continue at an increasing rate into the future (Pachauri et al., 2015). Warming temperatures have resulted in advancing phenologies of species (Parmesan and Yohe, 2003; Root et al., 2003). However, not all species are shifting at the same rate, as the timing of their life histories is controlled by different heritable and plastic cues (Thackeray et al., 2016; Visser and Gienapp, 2019; Roslin et al., 2021). Species from higher trophic levels, for example, show slower phenological shifts on average than species from lower trophic levels, likely because they are less sensitive to changes in climate (Thackeray et al., 2010, 2016). Differing rates of phenological change across species and trophic levels may decouple ecological interactions, creating resource mismatches between predators and prey that impact fitness and survival (Cushing, 1990; Visser and Both, 2005).

Mismatches between predator energy demands and prey availability during key life stages can impact fitness and survival of predators, sometimes leading to swings in adult abundance. Specifically, the match/mismatch hypothesis posits that the temporal mismatch between a predator and its prey during a critical life stage will decrease survival rates of the predator (Cushing, 1969, 1990). For example, egg-laying in great tits (*Parus major*) is advancing more slowly than their caterpillar prey, creating a mismatch between hatchling food requirements and peak caterpillar biomass that reduces nestling survival (Visser et al., 1998). Phenological mismatches have influenced fitness and survival of some species (Visser et al., 2006; Both et al., 2006; Plard et al., 2014) but not others (Durant et al., 2005; Pearce-Higgins et al., 2009; Ozgul et al., 2010). Changes in fitness or survival do not always translate to population-level impacts due to compensatory dynamics (Reed et al., 2013). Alarmingly, phenological mismatches are becoming increasingly common under climate change (Kharouba et al., 2018). As a result, there is an increasingly urgent need to determine if phenological mismatches will occur and to predict the impacts of a mismatch on survival and population dynamics.

1.1 Vulnerability to phenological mismatches

A key challenge in global change ecology is to understand how species and populations will respond to oncoming change (Sutherland et al., 2013; Parsons et al., 2014). Identifying relationships between species- and population-level traits and vulnerability to change is one avenue that has been used to identify sentinel species and prioritise species of conservation concern (Williams et al., 2008; Butchart et al., 2010). Vulnerability is determined by two factors: sensitivity and exposure (Williams et al., 2008), where sensitivity is determined by intrinsic traits such as physiological limits, ecological traits (e.g., behaviour), and genetic diversity; and exposure is determined by extrinsic factors filtered through local habitat and regional climate change. Identifying species- or population-specific vulnerability to mismatch is one option to identify those species or populations most likely to be impacted by phenological mismatch.

The vulnerability of a population to phenological mismatch is likely governed by the magnitude of a mismatch as well as the sensitivity of that population to mismatch. The likelihood of exposure and magnitude of a mismatch are influenced by a variety of factors. For example, a phenological mismatch is more likely to occur if prey have narrow temporal availability or limited abundance (Durant et al., 2005, 2007), if phenological mismatch is adaptive (Visser et al., 2012), or if predators use non-climatic environmental cues (e.g., photoperiod; Stenseth and Mysterud 2002) or traverse environments experiencing differing rates of climate change (e.g., altitudinal migrants; Inouye et al. 2000). Underlying physiological (e.g., body mass, metabolic rate, thermal tolerance), behavioural (e.g., prey specialization; Tucker et al. 2019) and life-history traits (e.g., age of maturation, voltinism; Ohlberger et al. 2014; Knell and Thackeray 2016), as well as physiological and behavioural plasticity, likely influence the sensitivity of a population to a mismatch. However, empirical evidence of differential sensitivity to mismatch is lacking (McLean et al., 2016; Thackeray et al., 2016). A clearer understanding of factors that mediate sensitivity to phenological mismatch could help predict which populations will be vulnerable to climate-driven changes in phenology. As climate change shifts the phenology of species, understanding the resilience or vulnerability of species and populations to phenological mismatches is of increasing importance, especially for species of cultural and commercial value (Cushing, 1990; Miller-Rushing et al., 2010; Thackeray et al., 2016).

1.2 Phenological change and mismatch in Pacific salmon

For migratory Pacific salmon (*Oncorhynchus* spp.), whose complex life histories unfold over multiple habitats and many thousands of kilometers, the matching of life-history events with suitable habitat and resources can be a particular challenge (Crozier et al., 2008). Juvenile salmon rear in freshwater lakes and streams for up to several years before they undergo smoltification and complete an energetically expensive non-feeding freshwater migration

that can extend over hundreds of kilometers and take up to several weeks to complete. They may spend up to several months replenishing energy stores and growing in the estuary before transitioning to the open ocean feeding grounds (Pearcy, 1992; Preikshot et al., 2012; Moore et al., 2016). Size and growth during this early marine period has been linked with survival, where larger and faster growing smolts are more likely to survive than smaller and slower growing smolts (Ward et al., 1989; Henderson and Cass, 1991; Beamish and Mahnken, 2001). Survival rates through this critical early marine phase can determine the number of adults that survive the marine environment and are recruited into the fishery (Pearcy, 1992). Therefore, salmon smolts that enter prey-replete estuaries and coastal regions, such as during a phenological match, can have higher survival. In fact, phenological mismatches can sometimes lead to a decrease in adult recruitment in Pacific salmon (Ryding and Skalski, 1999; Chittenden et al., 2010; Satterthwaite et al., 2014; Malick et al., 2015a), but this is not universally the case (Scheuerell et al., 2009; Irvine and Akenhead, 2013; Evans et al., 2014; Gosselin et al., 2018). Thus, phenological mismatches during this critical life stage can impact survival and population dynamics.

Climate change-driven environmental changes may result in increasing frequency of phenological mismatches between salmon and their prey. Ocean phenology of salmon prey is shifting at a rate at which salmon may be unable to track, potentially leading to phenological mismatches (Richardson, 2008). Globally, temperate spring phytoplankton and zooplankton phenology are advancing at rates in excess of 10 days/decade (Edwards and Richardson, 2004; Poloczanska et al., 2013), while in the subarctic Pacific zooplankton phenologies are advancing at rates as high as 14 days/decade (Mackas et al., 1998; Kahru et al., 2011). Climate warming has also resulted in earlier and more variable phytoplankton blooms and zooplankton biomass peaks in more southern regions, such as the Strait of Georgia in British Columbia, Canada (Allen and Wolfe, 2013; Mackas et al., 2013). Meanwhile, some salmon species may be shifting their outmigration phenology while others are not, leading to species-specific rates of phenological mismatch. In fact, a regionally-isolated study of pink (*O. gorbuscha*), coho (*O. kisutch*) and sockeye (*O. nerka*) salmon showed that pink salmon were advancing outmigration timing at ~5 days/decade, whereas sockeye and coho salmon from the same watershed were not altering their outmigration phenology (Kovach et al., 2013). These species-specific trends in outmigration phenology may not be representative of other, especially more southern, regions. Differing rates of phenological change between salmon and their prey will likely lead to phenological mismatches which may vary regionally and across species and populations, and could increase in frequency and severity under future climate warming scenarios.

1.3 Sensitivity to phenological mismatch

Certain traits may determine the sensitivity of salmon smolts to phenological mismatches with prey during the critical early marine stage. Salmon smolts complete a freshwater migration that may span great distances and depends upon endogenous energy stores which can approach very low levels (Rondorf et al., 1985; Stefansson et al., 2003). Individuals and populations with higher body condition may be more likely to survive and therefore less sensitive to periods of poor estuary or marine growth conditions associated with a phenological mismatch (Saloniemi et al., 2004; Persson et al., 2018). Energetic condition of smolts depends on experiences during freshwater rearing such as density dependence, habitat productivity, and environmental conditions (Beacham et al., 2014a; Freshwater et al., 2017; Carr-Harris et al., 2018; Jones et al., 2020). Indeed, rearing conditions can have carryover effects which can impact subsequent marine survival; larger smolts generally have higher survival rates than smaller smolts (Ward et al., 1989; Henderson and Cass, 1991; Beamish and Mahnken, 2001). Species and populations which have variable size and age at outmigration could exhibit differing degrees of sensitivity to phenological mismatch. Therefore, sensitivity to phenological mismatch could be an important tool for understanding when and how populations will be impacted by phenological mismatches.

In this thesis, I use a variety of approaches spanning data syntheses to targeted experiments, to assess the vulnerability of Pacific salmon to phenological mismatches[†]. In Chapter 2, I examine how smolt outmigration phenology of six species of anadromous and semelparous Pacific salmon has shifted across 66 populations spanning Alaska to Oregon. I then compare phenological shifts in salmon outmigration timing with marine phytoplankton bloom phenology to determine if salmon are tracking changes in the timing of vernal marine primary productivity. In Chapter 3, I combine two long term datasets of steelhead trout smolt outmigration timing and cold-water zooplankton phenology and abundance to examine how within- and across-year phenological mismatches could influence individual and outmigration cohort survival of steelhead trout. In Chapter 4, I use an experimental approach to determine condition-specific thresholds for prolonged swim performance and survival in a population of sockeye salmon. Finally, in Chapter 5, I compare physical and energetic condition of sockeye salmon smolts from different populations before and after freshwater migration. I then apply the relationship between Fulton's condition factor and prolonged swim performance developed in Chapter 4 to determine starvation resistance across populations, a proxy for sensitivity to starvation associated with phenological mismatch. Collectively these studies aim to elucidate how salmon species are changing their phenology, the impacts of phenological mismatches on survival, and whether body condition

[†]Here and throughout this document, prediction refers to model predictions, which explain data using statistical models.

can mitigate these impacts. Understanding which species are most vulnerable to phenological mismatches could help prioritise species for conservation and identify management interventions that could help mitigate the impacts of climate change-driven phenological mismatches.

1.4 Contributions

The data chapters of this thesis (Chapters 2, 3, 4, and 5) have been highly collaborative and have benefited from the wisdom, data, and hard work of countless scientists, many of whom are co-authors. Chapters 3, 4, and 5 have been either published or submitted to a journal for publication, while Chapter 2 has been prepared for publication. The reader will note that these chapters are written in the first-person plural to reflect the co-authors' contributions. For Chapters 2 and 3, I have benefited greatly from the data and knowledge gathered and held by various local, state, and federal organizations. Thus, the data are not my own, though I gathered, and collated them into several large datasets. For Chapter 4, I led the experiment, and, for Chapters 4 and 5, I led the lab analysis of samples, though I had significant help to complete both. For all data chapters, I was responsible for coding, analyzing the data, and writing the initial draft. All chapters benefited from the feedback and edits from my co-authors, data contributors, and committee members. Chapter 1 and 6 are my own and are therefore written in the first person singular.

Chapter 2

Variable phenological change and mismatch in Pacific salmon smolts

2.1 Summary paragraph

Global climate change is shifting the timing of life-cycle events, sometimes resulting in phenological mismatches between predators and prey (Cushing, 1990; Parmesan and Yohe, 2003; Root et al., 2003; Thackeray et al., 2010; Poloczanska et al., 2013; Visser et al., 2006). Phenological shifts and subsequent mismatches may be coherent across populations (Parmesan and Yohe, 2003), which would enable a "predict-and-prescribe" approach for improved conservation and management (Schindler and Hilborn, 2015), but alternatively could be variable and unpredictable across populations within the same species. For anadromous Pacific salmon (*Oncorhynchus* spp.), the survival of individuals from thousands of locally-adapted populations across diverse freshwater habitats depends upon juvenile migration timing to the Pacific Ocean relative to the availability of nearshore prey (Chittenden et al., 2010; Satterthwaite et al., 2014; Wilson et al., 2021). In fact, early marine phenological mismatches can determine marine survival and population dynamics for Pacific salmon (Malick et al., 2015a). Here we examine 66 populations across six anadromous Pacific salmon species throughout their range in Western North America, revealing differing rates in shifting salmon outmigration phenologies marked by significant within- and across-species variation. For example, we discovered that pink and chum salmon but not other Pacific salmon species had consistently advancing outmigration phenologies, while other species, such as coho salmon had more variable phenological shifts with many (17 of 26) advancing and some retreating (9 of 26). Despite testing numerous possible explanatory variables, variation in phenological shifts was not explained by changing environmental conditions or geographic patterns. Interestingly, outmigration phenologies have not tracked shifts in the timing of marine primary productivity, potentially increasing the frequency of future phenological mismatches. Unpredictable responses to climate change undermine the efficacy of predict-

and-prescribe approaches, and instead call for broader and more precautionary approaches to conservation of biodiversity and habitat.

2.2 Main

Shifts in the timing of life-history events, or phenology, are some of the most pervasive and well documented ecological impacts of climate change (Parmesan and Yohe, 2003; Root et al., 2003). Asynchronous shifts between consumers and their resources can result in phenological mismatches, potentially leading to reduced fitness and survival of consumers (Cushing, 1990; Visser and Gienapp, 2019; Visser et al., 2006, 1998). Rates of phenological change differ between species (Kovach et al., 2013), life histories (Winder and Schindler, 2004; Adrian et al., 2006), and trophic levels (Thackeray et al., 2010; Edwards and Richardson, 2004; Roslin et al., 2021); yet, within-species diversity in phenological shifts has rarely been documented. Within-species diversity in local adaptations across ranges and habitat types could drive stronger variation in phenological shifts among populations within a species than those observed among species (McLean et al., 2018). Understanding the coherence of phenological shifts both within and across species is imperative to understanding the predictability of phenological mismatches and climate change impacts.

Every year hundreds of billions of juvenile Pacific salmon (*Oncorhynchus* spp.) migrate from freshwater environments to the ocean, and their survival can depend upon how well their ocean arrival timing aligns with peak prey abundance (Chittenden et al., 2010; Satterthwaite et al., 2014; Wilson et al., 2021). Despite this common challenge, Pacific salmon occupy a vast diversity of freshwater habitats spanning biogeoclimatic zones, requiring seaward migrations of tens to thousands of kilometers. Consequently, there exists remarkable inter-population diversity in local adaptations, as well as incredible life history and phenological diversity (Carr-Harris et al., 2018). The timing of juvenile salmon emigrations varies greatly and is dependent upon both heritable and plastic traits (Crozier et al., 2011) that respond to species- and population-specific proximate and ultimate cues, including temperature, photoperiod, barometric pressure, and flow rates (Quinn, 2018). Both peak outmigration timing and within-population phenological diversity of Pacific salmon may be changing as a result of climate change, where either a shift in peak outmigration timing or a narrower range would increase the likelihood of a phenological mismatch with prey resources (Kovach et al., 2013). Indeed, some of the multifaceted drivers of salmon emigration timing, such as freshwater temperatures, may be changing asynchronously with the phenologies of marine prey, in response to climate change (Poloczanska et al., 2013; Edwards and Richardson, 2004; Allen and Wolfe, 2013). It is unclear if juvenile salmon outmigration timing is keeping pace with changes in marine prey phenology across their range (Kovach et al., 2013; Taylor, 2007; Otero et al., 2014).

Here we quantify phenological change in smolt outmigration phenologies and potential temporal mismatches with marine prey for all five species of anadromous and semelparous Pacific salmon in North America and steelhead trout (*O. mykiss*). We compiled and analyzed a unique dataset on smolt outmigration phenology containing data from 66 populations spanning 18 degrees latitude (~3500 km) from Alaska to Oregon, for a time series ranging between 1953 to 2020 (1858 years of data; Table 2.1). We paired this novel dataset with the vernal phenology of coastal Pacific Ocean primary productivity, as derived from satellite-inferred chlorophyll-a concentration (SeaWiFS, MODIS-A). Our goal was to quantify phenological change across populations from different species, determine whether phenological shifts could be predicted based on key biological, environmental, or geographic variables (Table 2.2) known to impact salmon outmigration phenology (Spence and Hall, 2010; Spence et al., 2014), and examine the possibility of increasing phenological mismatches through time.

2.2.1 Changes in smolt outmigration phenology

To determine the rate of phenological change for each population, we modelled yearly smolt emigration peak timing and temporal range (the number of days between the 25^{th} and 75^{th} percentile) and determined the rate of change for each metric across the timespan of the data (20 years minimum). Using a hierarchical state-space model framework, we estimated the peak outmigration date and its rate of change across years for each population. Site-specific variables (e.g., distance to the ocean, rate of spring temperature change) were used to determine if any variables correlated with changing smolt phenologies. We also examined how the temporal range in outmigration changed across years to test the possibility that the outmigration range was narrowing (Fig. 2.1).

Some species and populations exhibited high rates of phenological change, while others did not change substantially over the observed period (Fig. 2.1). Overall, 46 of the 66 observed salmon populations had advancing peak outmigration timing with 16 of those being statistically significant (95% confidence intervals did not span 0). Chum (*O. keta*) and pink (*O. gorbuscha*) salmon, which emigrate emigrate soon after emergence, had the fastest rate of advancement in outmigration timing (>5 days/decade; Fig. 2.1). Coho salmon (*O. kisutch*) and steelhead trout, which spend one or more years in freshwater after emergence, had much lower rates of change (0.1 days/decade and 0.5 days/decade, respectively). A combination of changes in environmental cues, shifts in life history, and genetic selection could be driving these species-specific shifts in smolt migration timing. For example, because of their lack of a prolonged freshwater rearing stage, pink and chum salmon could have outmigration phenologies that are more responsive to warming freshwater incubation temperatures, or shifts in adult migration/spawn timing (Taylor, 2007). Further, because pink and chum salmon have smaller juveniles that feed on lower trophic level prey than other salmon, they are likely more strongly impacted by shifts in marine zooplankton phe-

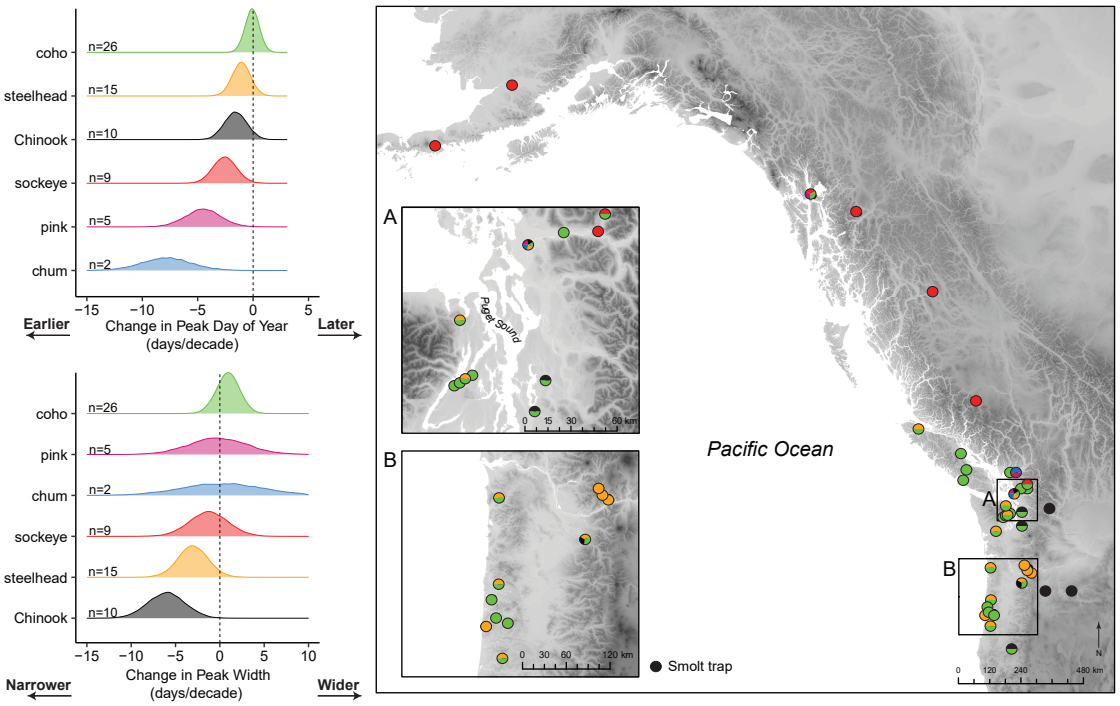

Figure 2.1: Location of smolt enumeration facilities (right) and shift in outmigration phenology (left, top) and migration temporal range (left, bottom) of six species of North American anadromous Pacific salmon (coho = green, pink = pink, chum = blue, steelhead = orange, sockeye = red, Chinook = black). Coloured circles represent species counted at that site. Site/species with more negative values are shifting to be earlier in the year, whereas those with more positive values are shifting to be later in the year.

nology (Malick et al., 2015a). System-specific studies of salmon outmigration phenology have also found species-specific changes. Peak outmigration timing of Auke Creek, Alaska coho salmon did not change over a 37-year period, whereas peak outmigration of Auke Creek pink salmon advanced at rates greater than 4 days/decade, and the peak outmigration of Atlantic salmon advanced at an average rate of 2.5 days/decade (Kovach et al., 2013; Taylor, 2007; Otero et al., 2014). Though species have different average rates of phenological change, we also revealed considerable unexplained within-species variability in phenological shifts.

We discovered variable and unpredictable patterns of phenological changes in Pacific salmon outmigration. While species explained some variation in the rate of change in peak outmigration phenology, the remaining variance was not explained by other geographic, environmental, or biological factors. We compared weighted linear models containing key geographic (e.g., latitude of the capture location, distance between the capture location and the ocean, watershed size), environmental (e.g., rate of change of mean, minimum, and maximum seasonal air temperatures, and precipitation) and biological (e.g., species, scale

of hatchery influence) variables. Since species could be responding differently, we included interactions between species and other predictor variables. Apart from an interaction between species identity and capture site elevation, no other variables or interactions clearly explained variability in the rate of change in peak smolt outmigration timing (see Section 2.3 Methods, Table 2.3). Thus, phenological change is inconsistent within species and appears unpredictable.

Among-species variability in the rates of phenological shifts was relatively low, while among-population variability remained high. In fact, the among-species variation accounted for only 40% of the total variation among populations (Fig. 2.2). For example, while on average coho salmon did not exhibit any phenological changes in outmigration timing, 17 of 26 populations were trending towards advancing phenology, with four populations significantly advancing; but 9 populations had the opposite pattern in phenology, with four populations significantly retreating. Thus, while there were species-level patterns, perhaps due to different intrinsic or extrinsic drivers of migration timing, there was even greater fine-scale population variation in migratory phenological change. It is likely that watershed complexity and different local manifestations of climate change create response diversity that cannot be predicted (Elmqvist et al., 2003). Furthermore, locally-adapted population traits could mediate the effects of both regional and large-scale climate drivers of phenological change. Phenological change is generally studied at the population level but too commonly reported as a species-level change, neglecting potential population variability (McLean et al., 2018). As a result, broad-scale climate change will likely manifest unpredictably in species with high local adaptability and response diversity, such as Pacific salmon.

Only steelhead trout and Chinook salmon exhibited changes in smolt outmigration range (Fig. 2.1), of which 11 of 15 steelhead trout populations (8 significantly), and 5 of 9 Chinook salmon populations (4 significantly) were trending narrower. Importantly, these two species have the most diverse life histories of the species under investigation, providing the greatest scope for loss of diversity. This lost phenological diversity could be driven by changing freshwater cues, selection against early or late migrants, or lost intra-population life-history diversity (Kovach et al., 2013) such as that driven by habitat contraction, decreased population abundance, and hatchery practices. Indeed, many populations of steelhead trout and Chinook salmon have decreased dramatically over the observed period (Losee et al., 2019), and have suffered widespread non-random habitat losses (McClure et al., 2008). Furthermore, though we focused on datasets enumerating predominately wild (unmarked) fish, offspring of adult hatchery strays are identified as wild and widespread hatchery propagation can influence genetic variation and outmigration timing (Sturrock et al., 2019). Human activities which decrease phenological diversity and narrow the outmigration window are likely to erode population-level resilience to phenological shifts in marine prey by increasing the likelihood of mismatches.

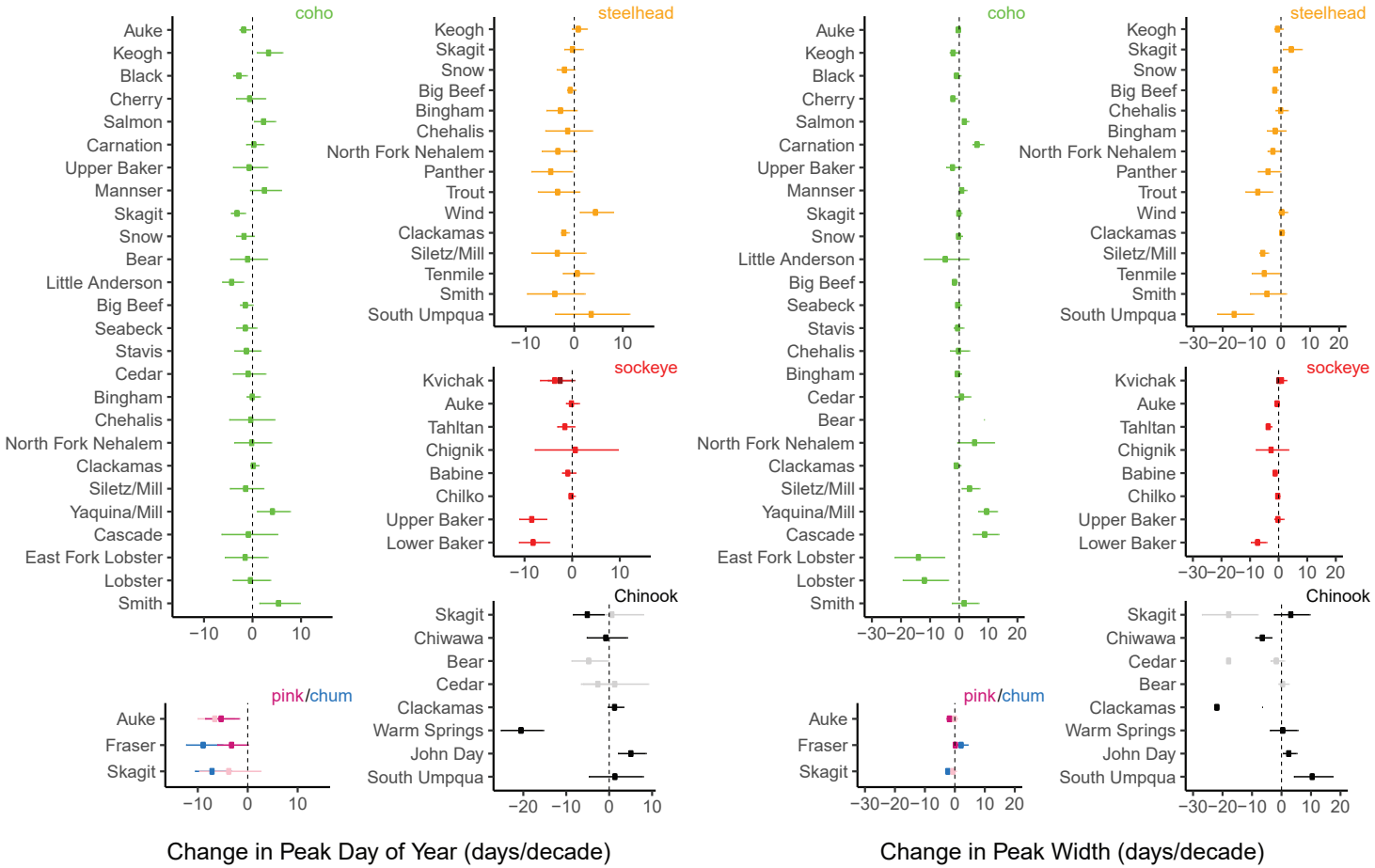

Figure 2.2: Shift in outmigration phenology (left) and change in temporal range of outmigration (right) of populations of six species of North American anadromous Pacific salmon (coho = green, even year pink = dark pink, odd year pink = light pink, chum = blue, steelhead = orange, sockeye = red, Chinook 1+ = black, Chinook 0+ = grey). Horizontal lines represent 95% confidence interval. Where 95% confidence interval overlaps with 0 (vertical dashed line), populations are not significantly changing outmigration date. Populations with more negative values are shifting to be early in the year/more narrow, whereas those with more positive values are shifting to be later in the year/wider outmigration range. Sites are ordered by latitude (north to south, top to bottom).

2.2.2 Phenological mismatch in juvenile salmon

We paired our smolt outmigration phenology dataset with satellite-derived estimates of spring phytoplankton phenology (SeaWiFS, MODIS-A; chlorophyll-a) to quantify the potential mismatch between salmon and the phenology of ocean prey. We compared the rate of change in peak smolt outmigration phenology between 1999 – 2019 to the rate of change in spring phytoplankton bloom across the 21-year time span in each corresponding coastal region. Spring phytoplankton phenology did not advance significantly in any regions corresponding coastal areas where salmon enter the marine environment (Fig. 2.4). However, in 9 of 38 coastal zones examined, average phytoplankton bloom phenology was advancing at rates greater than 8 days/decade; regions along the Oregon coast were experiencing faster rates of advancement. Due to these regional patterns in the rates of phenological shifts of primary productivity in the coastal ocean, salmon populations from coastal Oregon exhibited increasing phenological mismatch driven by disparity between the advancement of the spring bloom with salmon phenology not keeping pace. However, in more northern regions (i.e., Alaska, British Columbia), smolt migrations advanced faster relative to ocean phytoplankton phenology. Though there were regional trends, changes in peak outmigration did not deviate significantly from changes in spring phytoplankton bloom phenology (95% confidence intervals of the difference in the rate of change spans 0, where 0 indicates that salmon and phytoplankton phenology are shifting at the same rate; Fig. 2.3).

While both the spring phytoplankton bloom and salmon populations exhibited phenological shifts over the 20-year period, there was little correlation between them (correlation = 0.17), indicating that salmon outmigration timing is not tracking shifts in spring primary productivity. For example, salmon often had phenologies that were shifting while the corresponding spring phytoplankton bloom in their region was not shifting (Fig. 2.3). However, peak outmigration for 10 of 38 sites had increasing temporal mismatches throughout our recorded time series, with salmon outmigration phenology at 9 sites lagging behind the advancement of the spring phytoplankton bloom, and the remaining single salmon population outpacing the spring phytoplankton bloom at rates greater than 8 days/decade. Thus, more salmon are lagging behind spring phytoplankton phenological change rather than outpacing it. While salmon do not feed on phytoplankton, salmon marine survival is correlated with the timing of the spring phytoplankton bloom (Chittenden et al., 2010; Malick et al., 2015a; Wilson et al., 2021); the timing of the spring phytoplankton bloom signals the beginning of primary productive which cascades upward through trophic levels, to the zooplankton, icthyoplankton, and larval fish that do compose the differing juvenile salmon diets (Pope et al., 1994; Daly et al., 2014). Thus, we use phytoplankton phenology as a proxy for salmon prey phenology. Our study indicates that, despite the potential for increased survival during a phenological match with the spring Pacific Ocean phytoplankton bloom (Chittenden et al., 2010; Satterthwaite et al., 2014; Malick et al., 2015a; Wilson et al., 2021), salmon

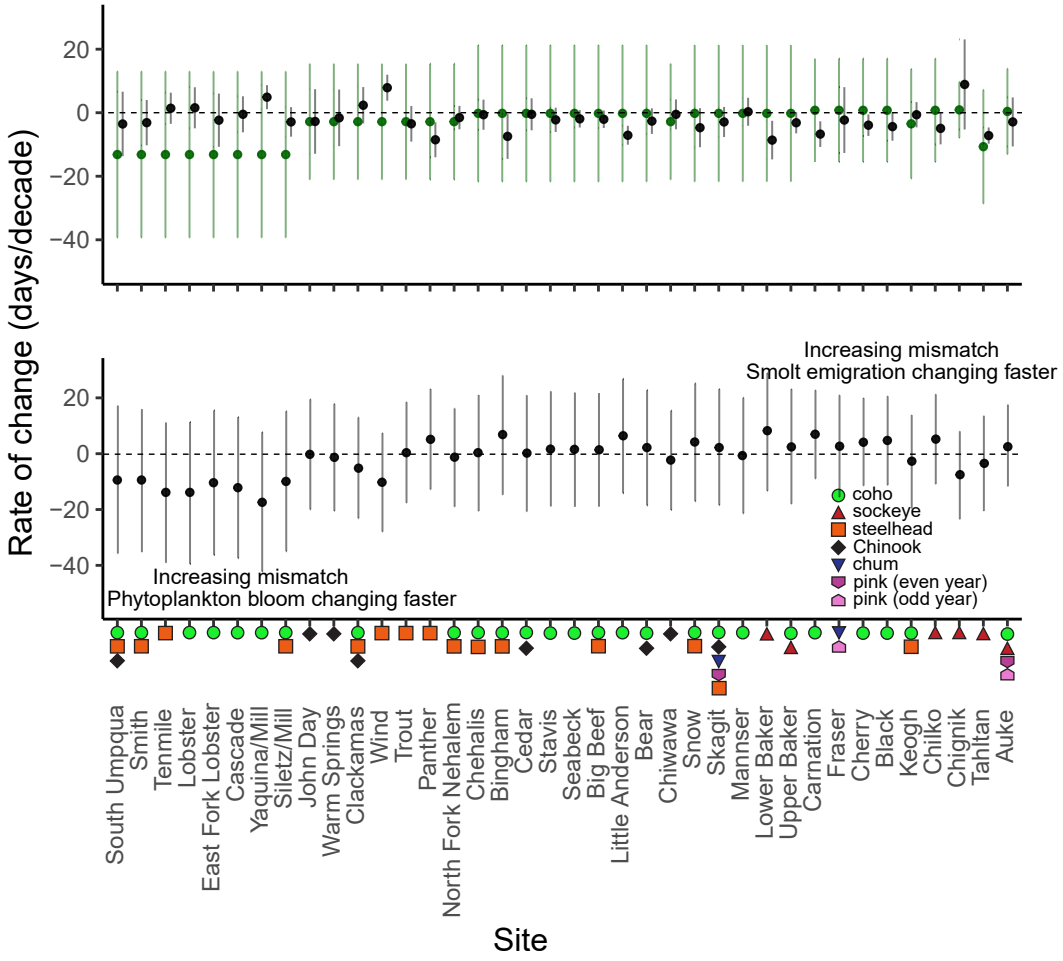

Figure 2.3: Rate of phenological change and mismatch. Top: Rates of phenological change averaged for all species at a given site (black) and for spring phytoplankton bloom (first date above 5% of the annual mean of satellite-derived chla concentration; green) between 1999 - 2019. Where 95% confidence interval overlaps 0 (horizontal dashed line) phenology is not significantly changing. Negative change means species are advancing, while positive change indicates species phenology is delaying to be later in the spring. Bottom: Relative rates of mismatch between spring phytoplankton bloom and salmon outmigration timing. Where 95% confidence interval overlaps 0 (horizontal dashed line) species phenologies are matching (shifting at the same rate). Negative change ($y<0$) indicates that the spring phytoplankton bloom is getting earlier relative to smolt migration, while positive change ($y>0$) indicates salmon outmigration is getting earlier relative to spring plankton phenology. Shapes indicate the salmon species that were monitored at that site. Sites are ordered by latitude (north to south, right to left).

outmigrations are not tracking changes in phytoplankton phenology, a harbinger of future phenological mismatches and decreased marine survival under climate change.

2.2.3 Conclusions

As the drivers of phenological shifts in Pacific salmon remain unclear, it is difficult to predict how salmon migration timing will respond to increasing climate change. In our analyses, most populations of salmon had advancing outmigration timing, with steelhead trout and Chinook salmon also exhibiting a narrowing outmigration range. Pink and chum salmon shifted migration timing to be earlier more rapidly than others, albeit with high inter-population variability. Examined geographic, environmental, and biological variables did not explain the rates of phenological change. Salmon outmigration appears to be under strong local control, such that cues and drivers of outmigration phenology may differ across watersheds, and no single predictor can account for broad patterns in smolt phenological shifts. However, we were unable to test fine-scale environmental or biological data as these data have not been collected across the geographic range of our data. Predicting population-specific phenological shifts and mismatches and their impact on species abundance and persistence, in relation to climate change and other anthropogenic disturbance remains untenable at present. Thus, rather than a 'predict-and-prescribe' approach to management of populations of salmon based on phenological mismatches with the early marine conditions, an alternative approach that acknowledges uncertainty and preserves salmon biodiversity would likely be more appropriate (Schindler and Hilborn, 2015). For species that are unable to keep pace with changes in prey phenology, conserving a range of habitats that supports species and population biodiversity provides the best potential for maintaining populations resilient to ongoing phenological changes and subsequent phenological mismatches. While globally coherent patterns of climate-driven phenological shifts reshuffle species interactions, local manifestations of climate change may be quite unpredictable as complex systems evolve and adapt.

2.3 Methods

2.3.1 Smolt migration datasets

North American Pacific salmon smolts are monitored annually throughout their range from Alaska to California, with smolts counted as they emigrate from natal freshwater rearing watersheds before entering the ocean. Smolts generally emigrate from rearing lakes, rivers, and streams during the spring or fall after spending anywhere between several weeks to several years in freshwater. Federal, State, and Indigenous governments in the United States and Canada, as well as community groups, have been monitoring smolt emigration since the mid-1950s. These monitoring programs intercept and enumerate smolts near-daily during the migration season using a variety of techniques such as full fence weirs, in which all

fish are counted, or using mark-recapture methods where a subset of fish are captured in traps (e.g., inclined plane trap, floating trap, rotary screw trap) or seines, and are marked, released, and captured again to determine abundance. Here, we collated data from 41 sites representing six species (66 site-species combinations or populations) of predominately wild (unmarked), spring emigrating Pacific salmon populations that had been monitored for >20 years, primarily seeking those that had limited hatchery influence, and counted wild smolts separately from hatchery produced smolts (1858 cumulative years across all sites and species). We refer to each site-species combination as a population throughout the manuscript, but recognize that some site-species combinations, particularly those at river mouths represent metapopulations, while those in the headwaters may represent partial populations.

2.3.2 Measuring phenological shifts

We modelled annual emigration for each species to identify peak and range of outmigration, and simultaneously fit a trend in peak day through time. In some populations, multiple juvenile life history forms with unique outmigration timing had been previously described, and so we provide separate estimates for them based on a date cut-off. Thus, several sites have two peaks described, one for each life history type. For each species and site, log daily abundance (either as raw counts, or as mark-recapture expanded estimates, depending on capture methodology and which count was the most accurate) for each year was modelled throughout the migration window using one of four state-space hierarchical models. We used state-space models to distinguish a data or observation model from the latent phenological trend. We considered four alternative process models for each dataset. Our simplest model used a normal approximation to describe the shape of the outmigration distribution.

$$f(x) = normal(\mu, \sigma_x) \tag{2.1}$$

Second, we used a Student-t distribution, which differs from the normal distribution in that when the degrees of freedom parameter is small, the Student-t distribution can have more extreme tails.

$$f(x) = Student - t(\mu, \nu, \sigma_x) \tag{2.2}$$

Application of either the normal or Student-t models assumes symmetry in the distribution of outmigration before and after the peak window. As a third model, we relaxed the assumption of symmetry and used a double normal distribution as a process model. The double normal distribution is widely used in fisheries to model quantities like selectivity (Methot and Wetzel, 2013). This distribution involves fitting two truncated normal distributions, joined by a common mean, but allowed to have different variances.

$$f(x) = \begin{Bmatrix} normal(\mu, \sigma_{x_1}), x < \mu \\ normal(\mu, \sigma_{x_2}), x > \mu \end{Bmatrix} \tag{2.3}$$

For the purposes of our application, this translates to the shape of outmigration before and after peak to be different. Finally, as a fourth model, we extended the double normal concept to a double Student-t distribution. This double Student-t differed from the double normal in allowing both the variance and degrees of freedom to differ between pre- and post- peak curves.

$$f(x) = \begin{Bmatrix} Student - t(\mu, \nu_1, \sigma_{x_1}), x < \mu \\ Student - t(\mu, \nu_2, \sigma_{x_2}), x > \mu \end{Bmatrix} \tag{2.4}$$

Equation 2.1 to Equation 2.4 describe process models fit to log daily smolt abundance in a single year, modelled by a distribution with a peak μ, and variance σ_x. Because each dataset in our analysis includes multiple years, the means, variances, and degrees of freedom ν in these equations can be further subscripted by year, allowing the parameters to change through time. For simplicity, we did not consider time-varying degrees of freedom for the Student-t or double Student-t model in Equation 2.2 and Equation 2.4. For the mean and variance parameters, we considered two hierarchical models. First, we developed models that allowed the means and standard deviations to be estimated as random effects:

$$ln(\mu_y) \sim normal(ln(\mu_0), \sigma_\mu) \tag{2.5}$$

$$ln(\sigma_y) \sim normal(ln(\sigma_0), \gamma_\sigma) \tag{2.6}$$

where $ln(\mu_y)$ is the log of the peak location parameter in year y, μ_0 is the estimated global mean across years, and σ_μ is the variation in peak dates. For the variance model, we also modelled random effects in log space so that σ_y is the standard deviation in year y (for example Equation 2.1 – Equation 2.2 above), $ln(\sigma_0)$ is the mean shape parameter, and γ_σ is the standard deviation among shape parameters. Because both trends are modelled in log space, these can be interpreted as exponential change in normal space. Treating either the means μ_y or variance parameters σ_y hierarchically assumes that these parameters are drawn from a common distribution.

While these random effects models are flexible, the focus of our inference is estimating phenological shifts, so we evaluated a separate series of random effect models that include trends in the mean and variance of these distribution:

$$ln(\mu_y) \sim normal(\mu_0 + \beta_\mu \cdot \nu, \sigma_\mu) \tag{2.7}$$

$$ln(\sigma_y) \sim normal(ln(\sigma_0) + \beta_\sigma \cdot \nu, \gamma_\sigma) \tag{2.8}$$

All other parameters are as before, but the inclusion of β_μ and β_σ allows for linear trends in the location and shape of these distributions through time. Equation 2.7 to Equation 2.8 describe changes for symmetric models with a single variance parameter (Equation 2.1 – Equation 2.2 above) – our models for asymmetric distributions allowed the pre- and post-peak shape parameters to have different estimated trends.

All models were fit separately to each dataset using maximum likelihood approaches, implemented in Template Model Builder (Kristensen et al., 2016) and R (R Core Team 2020). We used Akaike's Information Criterion (AIC; Akaike 1973) to identify models most supported by the data. In a handful of cases, models did not converge (generally because of too many missing years) and were excluded from consideration. We summarized output from these best fit models by computing the quartiles of the distribution in each year (the dates when 25% and 75% of fish had been counted), from now on referred to as the range of the data for each year. Annual range by year was modelled in a separate weighted linear model, where weight was assigned based on the inverse square of the variance.

2.3.3 Patterns in phenological shifts

We examined geographic, environmental, and biological variables for correlation with rate of change in peak outmigration phenology. Geographic variables were selected based on prior research linking variables to phenology (Spence and Hall, 2010; Spence et al., 2014; Sturrock et al., 2019) and were determined from ARCGIS using 30 m rasters and delineated watersheds. These variables included latitude of the capture location, distance to the ocean (distance between capture location and the ocean in km), capture location elevation and mean and maximum elevation of watershed above the capture location (in m), gradient (elevation of capture location divided by distance to the ocean), and watershed area above the smolt capture location (in km^2).

Environmental variables included the rates of minimum, mean, and maximum air temperature and precipitation change between first year of monitoring and 2013. These were calculated using the program ClimateNA (Wang et al., 2016). Briefly, latitude, longitude and elevation were estimated for random points that were placed in each watershed (1 for every 2 km^2 of watershed area, with points placed at least 500 m apart) using GIS. Latitude, longitude, and elevation for each point were used by ClimateNA to extrapolate monthly minimum, mean, and maximum air temperature and precipitation. We then averaged each variable for the summer (July to September), fall (October to December), winter (December to February), and premigration period (three months before peak outmigration for each population) for each year. Using a linear model approach, we determined rate of change as the slope of the relationship between seasonal variable (temperature or precipitation) across years.

Biological variables included species and a categorical variable describing local hatchery production. Species grouped all populations, no matter their age group, into one species.

Hatchery influence was determined using a scale where 0 indicated no hatchery in the watershed, no history of hatchery influence, nearest hatchery in a distant basin >100 km away; Category 1 had no current hatchery production of target species in watershed, but either (a) hatchery production in nearby watershed <100 km distant allowing for a low level of hatchery-origin strays, (b) some within basin hatchery production of target species in the distant past (e.g., >25 years ago), or both (a) and (b); Category 2 had ongoing, within basin hatchery production of target species in which natural-origin fish typically outnumbered hatchery-origin fish on the spawning grounds (proportion of Hatchery Origin Spawners [pHOS] <50%), and/or the number of natural-origin juveniles were comparable to, or greater than, the number of juveniles released from the hatchery. All or nearly all hatchery-origin fish were marked. Conservation hatchery programs employing a high proportion of natural-origin broodstock would likely be in this category; Category 3: Long history (multiple decades) of large-scale hatchery production in which hatchery-origin fish routinely outnumbered hatchery origin fish on the spawning grounds (i.e., pHOS > 50%), and/or the number of fish released from hatcheries was considerably greater than the number of natural-origin juveniles. Marking of hatchery-origin fish allows for assessment of hatchery demographics compared to natural population demographics.

2.3.4 Satellite-derived chlorophyll a

Remote-sensing satellite-derived chlorophyll-a concentration estimates (mg/m^3) were used as a proxy for phytoplankton abundance. We used level-3 processed daily global composites (9 km × 9 km) of surface chlorophyll-a concentration from two satellites, Sea-viewing Wide Field-of-view Sensor (SeaWiFS; 1999 – 2010) and the Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua; 2003 – 2019) from the Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov). Global daily composites were subset to 29 2° × 2° grid cells along the coast between 42 – 60°N, 161.5 – 124.5°W (Fig. 2.4). We concatenated daily composites into 8-day composites to limit missing data due to clouds. Finally, the 8-day composite surface chlorophyll-a concentration estimates for each 9 km × 9 km pixel were averaged to create an 8-day average for each grid cell. For overlapping years between 2003 – 2010, we compared 8-day average chlorophyll-a for each grid cell between SeaWiFS and MODIS-Aqua. Coefficients for grid cells was high, consistent with other studies (Malick et al., 2015a; Waite and Mueter, 2013). Therefore, for the overlapping years we used the average of composites from both satellites. Satellite chlorophyll-a estimates generally correspond with field observations of phytoplankton except during extremely high phytoplankton concentrations, which would not effect our estimate of spring phenology (Kahru et al., 2014). We used 2° × 2° grid cells, as these regions would encompass a large proportion of the early marine period for salmon. Additionally, coastal regions are prone to high spectral reflectance for SeaWiFS and MODIS-Aqua satellites (Kahru et al., 2014). Using

this method, we created sequential 8-day chlorophyll-a concentration estimates from Jan 1 to Aug 1 for 21 years spanning 1999 – 2019 for each grid cell.

We determined the annual spring phytoplankton bloom for each grid cell, and then calculated the rate of change in the bloom date across years. Spring phytoplankton bloom was defined as the first 8-day composite that was 5% above the annual mean for that grid cell (Foukal and Thomas, 2014). We used spring phytoplankton phenology as an indicator of the beginning of spring productivity in the ocean, and the initialization of a surge of spring productivity that spans trophic levels. However, trophic levels may have different rates of phenological change, which our approach would not capture (Thackeray et al., 2010; Edwards and Richardson, 2004). Rate of change in spring phytoplankton bloom date was then determined with a linear model of spring bloom date by year. Each salmon population was paired with the coastal region in which they would enter the ocean (i.e., marine entrance; Table 2.1).

2.4 Acknowledgments

This project would not have been possible without the dedication and fortitude of scientists and technicians from Alaska Department of Fish and Game, Fisheries and Oceans Canada, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, University of Washington, University of Oregon, Confederated Tribes of Warm Springs, and the United States Forest Service that collected the 41 long term datasets used in this project. We also thank Chelan County Public Utility District, King County Cooperative Watershed Management grant program, The WRIA 8 technical committee, Seattle Public Utilities, Puget Sound Energy, Bonneville Power Administration, Dingell-Johnson Sportfish Restoration Act, Washington State Salmon Recovery Funding Board, Washington State General Fund, and Seattle City Light for supporting these monitoring projects. Funding for S.M. Wilson was provided by Vanier Canadian Graduate Scholarship, Weston Family Scholarship, and Steven Berkeley Marine Conservation Fellowship. Additional funding from the Liber Ero Foundation was for J.W. Moore We also thank T.D. Williams, and members of the Salmon Watersheds Lab for feedback on the early manuscript.

2.5 Supplementary materials

2.5.1 Supplemental tables

Table 2.1: Candidate predictor variables for all smolt outmigration monitoring projects.

Site Name	Latitude	Longitude	Species (Hatchery Scale)	Years (range)	Years (number)	Distance to Ocean (km)	Elevation of Trap (m)	Elevation (m) (min, max)	Watershed Area (km^2)	Chlorophyll-a Section
Kvichak River	59.31	-155.94	sk(0)	1972 – 2001	25	56	15	160 (0, 2163)	2648	NA
Auke Creek	58.38	-134.63	sk(0), pk(0), co(0)	1980 – 2019	40	<1	21	235 (2, 583)	10	13
Tahltan Lake	57.98	-131.58	sk(0)	1984 – 2016	33	273.5	811	1014 (808, 1632)	37	11
Chignik Lake	56.26	-158.73	sk(0)	1995 – 2015	20	8	1	306 (0, 2505)	1623	26
Babine Lake	55.41	-126.68	sk(1)	1961 – 2002	35	434.5	709	1057 (316, 2581)	10,449	8
Chilko Lake	51.63	-124.14	sk(0)	1953 – 2014	59	690.1	1174	1634 (735, 3238)	16,741	4
Keogh River	50.67	-127.35	co(0), sthd(1)	1981 – 2015	35	<1	4	219 (3, 1190)	124	7
Black Creek	49.85	-125.10	co(1)	1978 – 2016	34	<1	1	102 (1, 468)	65	4
Cherry Creek	49.27	-124.78	co(1)	1992 – 2013	28	2	61	212 (59, 577)	13	4

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Site Name	Latitude	Longitude	Species (Hatchery Scale)	Years (range)	Years (number)	Distance to Ocean (km)	Elevation of Trap (m)	Elevation (m) (min, max)	Watershed Area (km^2)	Chlorophyll-a Section
Fraser River	49.13	-122.30	ch(0), pk(0)	1966 – 2016	28	26.5	5	1188 (1, 3955)	231,524	4
Salmon River	49.12	-122.57	co(1)	1986 – 2009	23	14	30	67 (1, 148)	85	4
Carnation Creek	48.92	-125.00	co(1)	1982 – 2015	34	<1	5	293 (3, 902)	113	4
Upper Baker Lake	48.65	-121.69	co(3), sk(3)	1989 – 2018	30	92	218	1103 (211, 3280)	19	3
Lower Baker Lake	48.55	-121.74	sk(3)	1989 – 2018	30	78	127	1010 (49, 3280)	8	3
Mannser Creek	48.53	-122.04	co(2)	1994 – 2016	23	43.4	25	132 (23, 434)	6	3
Skagit River	48.44	-122.34	pk(0), ch(2), co(2), ck(2), sthd(2)	1990 – 2019	30	17	1	1060 (211, 3280)	1172	3
Snow Creek	47.98	-122.89	co(1), sthd(1)	1978 – 2016	38	<1	6	386 (3, 1279)	60	3
Chiwawa River	47.79	-120.66	ck(3)	1999 – 2019	20	830.3	562	1330 (562, 2734)	488	2
Bear Creek	47.67	-122.11	co(1), ck(1)	1999 – 2019	20	48.6	13	106 (9, 192)	122	3
Little Anderson Creek	47.66	-122.76	co(1)	1994 – 2019	24	<1	5	117 (5, 167)	12	3

(Continued on next page...)

Site Name	Latitude	Longitude	Species (Hatchery Scale)	Years (range)	Years (number)	Distance to Ocean (km)	Elevation of Trap (m)	Elevation (m) (min, max)	Watershed Area (km^2)	Chlorophyll-a Section
Big Beef Creek	47.65	-122.78	co(1), sthd(1)	1978 – 2019	42	<1	4	146 (2, 392)	32	3
Seabeck Creek	47.64	-122.84	co(1)	1993 – 2019	27	<1	5	114 (3, 184)	13	3
Stavis Creek	47.62	-122.88	co(1)	1993 – 2019	27	<1	7	125 (4, 187)	16	3
Cedar Creek	47.48	-122.20	co(1), sthd(1)	1999 – 2019	20	34	10	589 (5, 1662)	483	3
Bingham Creek	47.15	-123.40	co(1), sthd(1)	1982 – 2013	32	66.3	76	170 (75, 869)	154	3
Chehalis River	46.80	-123.16	co(2), sthd(2)	2000 – 2020	20	85	28	242 (27, 1165)	2545	3
North Fork Nehalem River	45.81	-123.74	co(3), sthd(3)	1998 – 2017	20	20.6	88	271 (85, 737)	111	2
Trout Creek	45.80	-121.93	sthd(1)	1995 – 2016	20	266.5	330	716 (267, 1365)	88	2
Panther Creek	45.77	-121.84	sthd(1)	1995 – 2016	20	251.8	181	705 (96, 1506)	107	2
Wind River	45.72	-121.80	sthd(1)	1995 – 2016	21	245	25	702 (23, 1630)	581	2
Clackamas River	45.24	-122.28	co(2), ck(2), sthd(1)	1959 – 2015	57	246	203	1028 (201, 2199)	1727	2
Warm Springs River	44.87	-121.09	ck(3)	1993 – 2019	33	462.1	409	951 (378, 1702)	1122	2

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Site Name	Latitude	Longitude	Species (Hatchery Scale)	Years (range)	Years (number)	Distance to Ocean (km)	Elevation of Trap (m)	Elevation (m) (min, max)	Watershed Area (km^2)	Chlorophyll-a Section
John Day River	44.84	-119.80	ch(1)	1979 – 2017	23	574	535	1379 (556, 2759)	12,379	2
Siletz/Mill River	44.74	-123.79	co(1), sthd(3)	1997 – 2019	23	110.8	50	337 (49, 953)	168	1
Yaquina/Mill River	44.57	-123.91	co(1)	1997 – 2019	22	30.7	45	219 (43, 499)	10	1
Cascade River	44.32	-123.85	co(1)	1998 – 2019	21	61.4	52	205 (52, 577)	14	2
East Fork Lobster River	44.25	-123.64	co(1)	1988 – 2019	32	65.6	208	553 (210, 1042)	15	1
Lobster River	44.25	-123.64	co(1)	1988 – 2019	31	65.6	195	433 (195, 670)	17	1
Tenmile River	44.22	-124.11	sthd(1)	1992 – 2016	25	<1	11	335 (3, 752)	60	1
West Fork Smith River	43.81	-123.77	co(1), sthd(1)	1998 – 2019	22	56.8	58	285 (56, 867)	68	1
South Umpqua River	42.98	-122.86	ck(1),sthd(2)	1991 – 2016	24	308.8	350	989 (350, 2051)	630	1

Species names are abbreviated as follows sk = sockeye, pk = pink, co = coho, ch = chum, ck = Chinook salmon, sthd = steelhead trout.

Chlorophyll-a section refers to the map sections on Fig. 2.4.

Table 2.2: Variables and associated hypotheses.

Variable	Hypothesis
Latitude	Climate driven warming is occurring faster at higher latitudes in both freshwater and marine habitats, which may lead to higher rates of phenological shifts in northern compared to more southern populations. Additionally, populations at different latitudes use different cues that could change at different rates due to climate change (Spence and Hall, 2010; Spence et al., 2014).
Species	Given different species life histories (i.e., age at outmigration), different use of cues, and different habitat and prey preference, species could have different rates of changes in outmigration timing (Taylor, 2007; Kovach et al., 2013).
Trap Elevation	Salmon may not be able to access all areas of the watershed. Trap elevation represents an approximation of the elevation where salmon may rear, where a trap at a moderate elevation may be experiencing different shifts in the hydrograph compared to a coastal or high elevation collection site (Spence et al., 2014).
Max Watershed Elevation above the trap	Watersheds with higher elevations are likely experiencing higher rates of climate change resulting in larger phenological shifts (Spence et al., 2014).
Mean Watershed Elevation above the trap	Watersheds of moderate elevation may be shifting from snow dominated to rain dominated hydrographs, changing the timing of peak flows, a cue for outmigration timing (Spence et al., 2014).
Distance to the Ocean	Collection and thus rearing locations that are further from the ocean likely use migratory cues that may become disconnected from ocean prey phenology through differential rates of climate change across increasingly distant regions.
Work (Elevation x Distance)	Fish in habitats experiencing climate that is changing at different rates than the estuary/coastal marine environment may be less able to track changes in marine prey phenology due to use of more static (i.e., photoperiod) cues or cues that may be becoming less predictive (i.e., temperature) of ocean prey phenology.
Area	Larger watersheds could incorporate more diverse habitat and more populations, making them less likely to exhibit strong phenological shifts.

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Variable	Hypothesis
Hatchery Category	Populations closer to hatcheries or with more adult hatchery strays are more likely to experience genetic changes as a result of wild-hatchery inter-breeding (Sturrock et al., 2019).
Rate of change of Fall Temperatures	Increased fall temperatures could lead to longer growing seasons and larger, earlier migrating smolts (Quinn, 2018).
Rate of change of Summer Temperatures	Increased summer temperatures could result in increased mortality, leading fish to emigrate younger. These fish may leave later to allow for additional spring growth (Quinn, 2018).
Rate of change of Spring Temperatures	Increased spring temperatures could lead to earlier freshets and signal earlier outmigration timing (Kovach et al., 2013; Otero et al., 2014; Spence et al., 2014; Kennedy and Crozier, 2010).
Rate of change of Winter Temperatures	Warmer winter temperatures could lead to improved growing conditions and earlier spring outmigration, especially for pink and chum salmon (Quinn, 2018).
Rate of change of Fall Precipitation	Increased fall precipitation could lead to increased growing opportunities due to increased habitat and flushing rates, leading to earlier spring outmigration timing (Quinn, 2018).
Rate of change of Summer Precipitation	Decreased summer precipitation could lead to increased mortality, leading fish to emigrate younger. These fish may leave later to allow for additional spring growth (Quinn, 2018).
Rate of change of Spring Precipitation	Increased spring precipitation could lead to an earlier increase in flows, which could lead to earlier outmigration timing (McCormick et al., 1998; Otero et al., 2014; Spence et al., 2014).
Rate of change of Winter Precipitation	Decreased winter precipitation could lead to decreased flows and increased mortality, leading fish to emigrate younger. These fish may leave later to allow for additional spring growth (Quinn, 2018).

Table 2.3: Top model (<2 ΔAIC) and predictor coefficients.

Model Rank	Terms	Coefficients (95% CI)
Species * Trap Elevation (m)	Species - Chinook	-0.4240 (-0.8556, 0.0077)
	Species - Chum	**-0.6929 (-1.2812, -0.1045)**
	Species - Coho	**-0.2130 (-0.3291, -0.0969)**
	Species - Pink	-0.2048 (-0.9599, 0.5504)
	Species - Sockeye	-0.1581 (-0.4774, 0.1613)
	Species - Steelhead	-0.0156 (-0.1244, 0.1557)
	log(Trap Elevation)	**0.0997 (0.0095, 0.1899)**
	Chum:log(Trap Elevation)	-0.2100 (-0.7368, 0.3167)
	Coho:log(Trap Elevation)	-0.0462 (-0.1428, 0.0503)
	Pink:log(Trap Elevation)	-0.2099 (-0.5294, 0.1097)
	Sockeye:log(Trap Elevation)	-0.0819 (-0.1847, 0.0210)
	Steelhead:log(Trap Elevation)	**-0.1374 (-0.2358, -0.0391)**

Bold items indicate a significant effect, where the 95% confidence interval (95% CI) does not span 0.

Table 2.4: P values of Bonferroni post hoc pairwise comparisons of the rate of change in peak phenology across species.

	Chinook Salmon	Chum Salmon	Coho Salmon	Pink Salmon	Sockeye Salmon
Chum Salmon	0.176				
Coho Salmon	1.0	**0.018**			
Pink Salmon	1.0	1.0	0.149		
Sockeye Salmon	1.0	0.268	1.0	1.0	
Steelhead Trout	1.0	0.051	1.0	0.478	1.0

Bold items indicate a significant effect with a $\alpha = 0.05$.

2.5.2 Supplemental figures

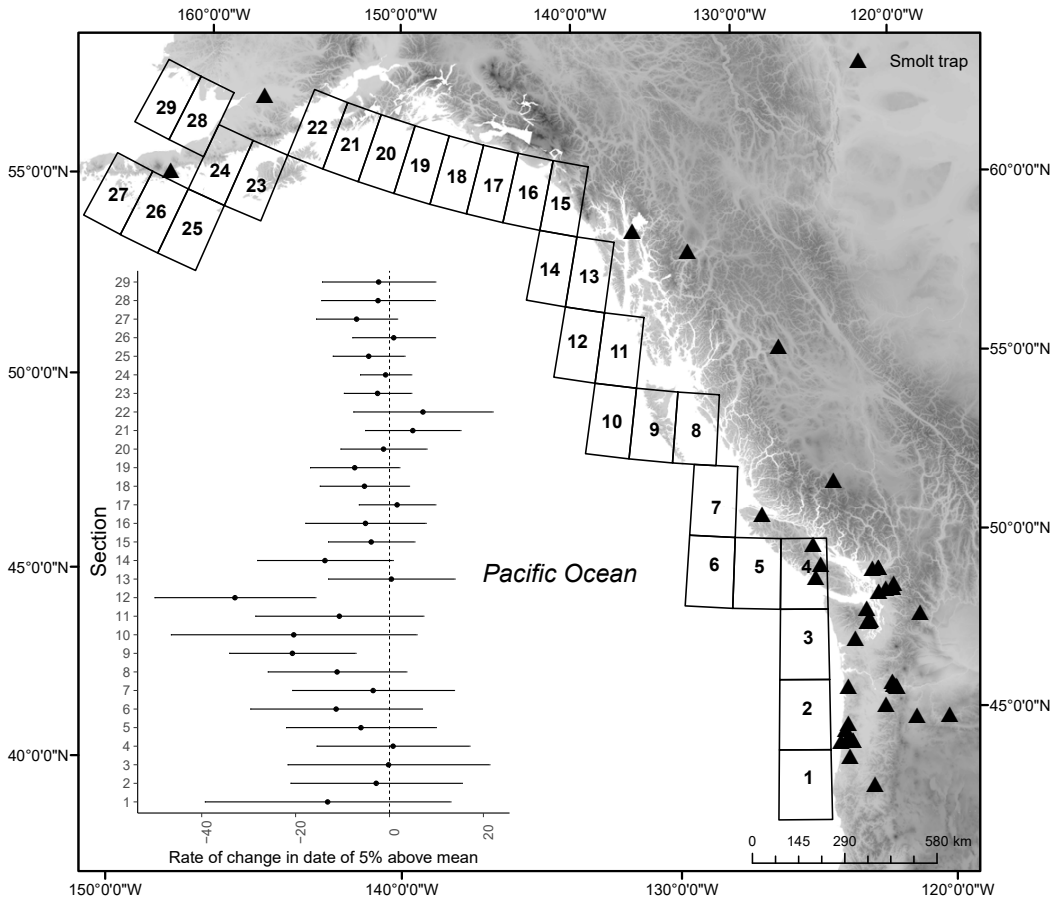

Figure 2.4: Map of satellite derived chlorophyll-a 2 × 2 degree sections 1 – 29, with trap locations (black triangles). Inset is the rate of change in initial peak of chlorophyll-a (first day above the 5% of the annual mean chlorophyll-a) for each section with 95% confidence intervals.

Chapter 3

Phenological mismatch, carryover effects, and marine survival in a wild steelhead trout population

3.1 Abstract

Climate-driven changes in the oceans, such as shifts in prey timing and abundance, could influence variability in population productivity of marine fishes. For example, according to the match/mismatch hypothesis, the temporal matching of the young salmon outmigration from freshwater to the ocean relative to the timing of availability of their prey could influence their marine survival. Indeed, understanding patterns and processes of marine survival is particularly pressing in many salmon and steelhead trout populations due to recent declines. To determine whether phenological mismatches between juvenile salmonids and their prey could contribute to low ocean survival, we analyzed the migration timing and ocean survival of 22,116 tagged juvenile steelhead trout (*Oncorhynchus mykiss*) over 12 years from the Wind River, Washington State, USA. We used a Bayesian multilevel modelling approach with variable selection to assess how survival was associated with body size, river exit date, the biological spring transition date (the day when northern zooplankton first appeared in the coastal region near the Columbia River estuary), and the degree of mismatch (the effect of the interaction between individual outmigration timing and biological spring transition date). The variables with the highest probability of contributing to individual survival were fish size (100%), river exit date (99%), the interaction between year and river exit date (91%), and the biological spring transition date (64%). Fish that were larger than aver-

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age at outmigration had higher ocean survival, providing further evidence that freshwater growing conditions have carryover effects on marine survival. Years with greater annual phenological mismatches such as those years with late biological spring transition dates (i.e., occurring after June 1st), or warm sea surface temperatures, had sufficiently low marine survival to compromise recovery goals. Substantial intra-annual variation in outmigration timing buffered the population from inter-annual variation in optimal outmigration timing. Collectively these findings indicate that freshwater growing conditions, migration timing, and the timing of high-quality food availability in the nearshore coastal environment work in concert to influence individual survival and annual smolt-to-adult returns.

3.2 Introduction

There is a need to understand how shifting ocean conditions influence variability in the productivity of commercially, recreationally, and ecologically important fishes. Marine fish population productivity is linked with size-dependent survival in early life history stages, which may depend on the timing and abundance of suitable prey for somatic growth (Anderson, 1988; Hjort, 1914). Therefore, timing and abundance of prey during early life stages likely elicits bottom-up control of population productivity (Platt et al., 2003; Ware and Thomson, 2005). Understanding the effects of variable timing and abundance of prey on individual survival could increase predictability of population productivity, especially in the face of a changing climate (Cushing, 1990). Specifically, the match/mismatch hypothesis has been used to explain variability in marine fisheries productivity through examining the timing and abundance of prey relative to the predator phenology. It postulates that when prey are abundant during a sensitive life-history stage of the predator, predator survival will be higher than average, but if predator and prey phenology become out of sync, predator survival will decrease (Cushing, 1969, 1990). For example, Durant et al. (2005) found that a phenological mismatch between food and food requirements decreased survival in Atlantic cod (*Gadus morhua*). However, not all individuals/species are equally sensitive to phenological mismatches. Sensitivity to mismatches may be influenced by intrinsic traits such as body condition, which are affected by experiences in other life stages (i.e., carryover effects; Anderson et al. 2013; Thackeray et al. 2016). For example, larger individuals could withstand greater phenological mismatches than smaller individuals with presumably poorer body condition (Ohlberger et al., 2014). Thus, the match/mismatch hypothesis is an important framework in this era of increasing climate change-driven variability, and is likely one of several key components for understanding how ocean conditions control productivity of marine fish populations.

Variability in ocean survival has resulted in extreme population swings in migratory Pacific salmon (*Oncorhynchus* spp.), likely shaped in part by climate-driven changes in prey abundance during the first few months at sea. For example, Mantua et al. (1997) found

that during positive phases of the Pacific Decadal Oscillation (PDO) Alaskan salmon populations had a 200% increase in adult returns, likely caused by warmer ocean temperatures resulting in higher zooplankton (food) abundance for young salmon. However, the relationship between PDO and salmon recruitment was much weaker in more southern populations such as those of the Columbia River since zooplankton dynamics for the Washington and Oregon coast are influenced by different environmental conditions than in Alaska (Gargett, 1997). Other oceanic correlates representing processes occurring on varying temporal and spatial scales, including El Niño Southern Oscillation (ENSO), North Pacific Gyre Oscillation (NPGO), sea surface temperature, salinity, and upwelling, have been associated with salmon population dynamics, contingent on the scale at which they were tested (Francis and Hare, 1994; Kilduff et al., 2015; Malick et al., 2015b; Mueter et al., 2005; Nickelson, 1986; Pearcy, 1992; Scarnecchia, 1981). Environmental conditions (e.g., sea surface temperature, salinity, upwelling strength) occurring within 1000 km from the river mouth are often more strongly correlated with salmon survival and productivity than environmental conditions that persist at larger temporal and spatial scales (Malick and Cox, 2016; Mueter et al., 2007, 2002b,a), supporting the hypothesis that ocean conditions experienced during the first few months at sea can strongly influence salmon productivity. The strength of the correlation between local food abundance and survival suggests that bottom-up control during the early marine period is a strong driver of survival. However, it is less clear what role, if any, the timing of food availability and/or phenological synchrony with juvenile salmon outmigration may play in restricting survival through this period.

There is some evidence that match/mismatch dynamics may contribute to ocean survival of salmon. Salmon that enter the marine environment during peak food (zooplankton) availability grow faster (Fiechter et al., 2015; MacFarlane, 2010) and because growth during early marine residence is highly correlated with survival to adulthood (Beamish and Mahnken, 2001; Friedland et al., 2014), it is likely that the matching of smolt ocean entry and peak prey abundance influences salmon survival and productivity (Chittenden et al., 2010; Ryding and Skalski, 1999; Satterthwaite et al., 2014). However, the few studies that have looked at survival as a function of salmon migration timing relative to prey abundance have had mixed results. Scheuerell et al. (2009) found that for both Snake River Chinook salmon (*O. tshawytscha*) and steelhead trout (*O. mykiss*), migration timing was important for survival, however the timing of the spring upwelling transition date (the date that Ekman transport switches from primarily downwelling to primarily upwelling in the spring, and a proxy for the timing of the spring phytoplankton bloom) was not an important driver of survival. Salmon migrating in early to mid-May had $4 - 50$ times higher survival than fish migrating in mid-June, regardless of changes in the spring upwelling transition date. However, timing of the spring upwelling transition date was an important predictor of survival for hatchery coho salmon (*O. kisutch*) (Ryding and Skalski, 1999), though this relationship may have changed over time (Rupp et al., 2012). Further, ocean survival was highest when

hatchery Chinook salmon from California's Central Valley were released within 70 – 115 days of the upwelling transition date; evidence that a phenological match increased survival (Satterthwaite et al., 2014). Using phytoplankton as a more direct proxy of zooplankton prey availability, Chittenden et al. (2010) found that hatchery coho salmon from British Columbia, Canada had 1.5 – 3 times higher survival when smolts were released coinciding with peak marine phytoplankton productivity. Similarly, changes in the timing and abundance of local phytoplankton blooms were related to the number of adult pink salmon (*O. gorbuscha*) that return to freshwater (Malick et al., 2015a). Thus, there is evidence that a phenological mismatch affects survival of Pacific salmon in some systems. However, most of these studies were on hatchery fish, which are genetically, morphologically, physiologically, and behaviourally different than wild fish (Naish et al., 2007; Swain et al., 1991). Hatchery fish often have lower marine survival than wild salmon (Jonsson et al., 2003) and may respond differently to match/mismatch with prey, possibly as a result of their lack of life history and phenological diversity (Sturrock et al., 2019). Therefore, there is an important knowledge gap with regards to potential impacts of match/mismatch dynamics, especially for wild salmon survival.

Somatic growth rates and subsequent survival in the early marine environment may be influenced by preceding freshwater conditions that carry over to the ocean environment. Freshwater conditions (e.g., habitat quality, temperature, density dependence) control body size and condition of smolts (Bailey et al., 2018; Rich et al., 2009; Schindler et al., 2005), with larger smolts generally having higher ocean survival than smaller smolts (Duffy and Beauchamp, 2011; Healey, 1982; Henderson and Cass, 1991; Ward et al., 1989). Thus, changes to the freshwater environment that alter fish growth and body size can subsequently impact ocean survival. For example, climate change-driven warming has altered growth and life-history patterns of Bristol Bay sockeye salmon (*O. nerka*) smolts from Alaskan Lakes; smolts now are younger and substantially smaller than those from even 20 years ago (Rich et al., 2009; Schindler et al., 2005). This shift was accompanied by a decrease in overall ocean survival rates and population productivity (Tillotson and Quinn, 2016). Freshwater growing conditions could also influence trade-offs associated with the timing of smolt outmigration. For slower-growing fish, migrating later in the season allows for more freshwater growth which increases size at outmigration in order to reach a smolt size that is viable in the ocean. However, this freshwater growth comes at a cost of lost ocean growth opportunities and a delay in outmigration timing, which may decrease survival (Mortensen et al., 2000). Thus, freshwater growing conditions may influence both size as well as timing at outmigration. Furthermore, the effect of phenological mismatch could be size-dependent (Ohlberger et al., 2014), such that matching with food availability in the early marine environment is more important for smaller fish which may be more sensitive to mismatches than larger fish. Freshwater growing conditions can influence size at outmigration which

impacts marine survival of migratory salmonids, and the strength of this effect may depend on ocean feeding conditions during the first few months at sea.

Understanding the underlying processes and temporal patterns of marine survival is of timely importance for many salmon and steelhead trout populations given recent population declines and subsequent imperiled conservation status. For example, declines in ocean survival rates of steelhead trout have contributed to declining population trends that have sparked conservation concerns (Kendall et al., 2017). In 2017, a record low return of adult Chilcotin and Thompson River steelhead trout (58 and 177, respectively) in British Columbia, Canada, representing an 80% decline in population size over the last three generations, led the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to conduct an emergency assessment which found the populations to be at imminent risk of extinction ('Endangered' designation; COSEWIC 2018), and stakeholders are now urging the Canadian Government to list these populations under the Canadian Species At Risk Act (SARA; Whitemore and Sandborn 2018). Indeed, 80% of steelhead trout populations in the Pacific Northwest have declined in the past 40 years, and decreases in marine survival are likely a strong contributor to these spatially coherent population declines (Kendall et al., 2017; Ward, 2000). For example, smolt-to-adult survival rates decreased from 15% on average before 1990 to just 3.5% for the Keogh River steelhead trout population in British Columbia, Canada (Ward, 2000). Such dramatic decreases in marine survival have led to closures of freshwater recreational fisheries and challenged other fisheries management and recovery efforts. In the Columbia River Basin alone, >$500M USD per year is invested into a fish and wildlife program largely devoted to the recovery of salmon and steelhead trout affected by dams (NPCC, 2017). However, current recovery scenarios depend upon smolt-to-adult return rates (SAR) for steelhead trout and spring Chinook salmon averaging a minimum of 4% (2 – 6% inter-annual range; NPCC 2014), targets which are not regularly being met for the majority of populations (McCann et al., 2016). If marine survival decreases below the levels included in recovery scenarios, steelhead trout populations will likely continue to decline unless other sources of mortality are further decreased (McCann et al., 2016). Thus, studies that examine how potential factors, such as phenological mismatch with ocean prey and/or freshwater carryover effects, influence marine survival of steelhead trout populations are relevant to informing management and recovery efforts and targets.

Here we investigated how ocean survival of wild salmon is influenced by the potential match or mismatch of their outmigration timing with ocean prey availability as well as other potential factors. We addressed this question using an extensive dataset spanning 12 years and including over 22,000 individually-marked wild steelhead trout smolts from the Wind River, a tributary of the Columbia River (Washington State, USA). We used a multi-level model that included both annual variables and within-year variables thought to possibly affect individual smolt ocean survival. Each variable had an associated *a priori*

hypothesis (Table 3.1). For example, we predicted that larger individual fish would have higher survival than smaller fish. Further, based on the match/mismatch hypothesis, we predicted that timing of outmigration and prey availability would influence the individual and annual patterns of survival. Using annual data on the biological spring transition date (the first day northern and energy-dense zooplankton were found off the Oregon coast; Miller et al. 2017), we predicted that there would be an optimal biological spring transition date, which would result in the highest annual survival probability (annual mismatch hypothesis). We also hypothesized that there would be an optimal outmigration date within each year that would result in the highest individual survival probability and that this optimum would differ based on the biological spring transition date (individual mismatch hypothesis). We discovered that in years where the biological spring transition date was earlier, cohort survival was higher (annual mismatch hypothesis), but within a year, fish that emigrated closer to the biological spring transition date did not always have higher survival (individual mismatch hypothesis).

For the second phase of model selection, the Annual Covariate Inclusion Model, we compared eleven correlated annual variables (e.g., biological spring transition date, PDO) and demonstrated that multiple annual variables impacted survival including sea surface temperature, spring upwelling transition date, PDO and the ecosystem indicator. Thus, in addition to individual-level variables, growing conditions in the ocean were important predictors of steelhead smolt survival.

3.3 Methods

We combined data from two existing long-term datasets to determine if individual and annually-averaged ocean survival of steelhead trout smolts were related to size (fork length), outmigration timing, cold-water affiliated (northern) copepod biomass, and individual and/or annual phenological mismatch. We used individual size, outmigration date, and survival data of >22,000 individually-marked Wind River steelhead trout, collected by the Washington Department of Fish and Wildlife, as well as the biomass of northern copepod taxa and the biological spring transition date, collected by NOAA Northwest Fisheries Science Center. We combined these two datasets and ran an integrated multilevel model with variable selection terms to determine parameter inclusion probabilities. Multilevel models incorporate fixed and random effects that are nested within multiple groups. In our case, we had two groups: an individual-level model that estimated individual survival probabilities, nested within a group-level model that estimated annual survival probability. This accounted for the non-random probability of survival due to shared conditions (explained/fixed and unexplained/random) throughout the steelhead trout life cycle, while also enabling examination of factors that operate at the within year/individual-level scale. For the first phase of model selection, hereafter, the Biological Spring Transition Date Model, the group-level fixed ef-

Table 3.1: Variable definitions and associated hypotheses.

Variable	Abbrev.	Hypothesis	Reference
River Exit Date	RE	Outmigration timing matters, regardless of the timing of the biological spring transition date.	Ryding and Skalski 1999; Scheuerell et al. 2009
River Exit Date Squared	RE^2	There is an optimal outmigration date, where probability of survival starts low, increases to an optima, and decreases across river exit dates.	Scheuerell et al. 2009
Individual Mismatch	RE^*Year	The optimal timing of outmigration varies across years in correspondence with the phenology of ocean prey.	Scheuerell et al. 2009; Satterthwaite et al. 2014; Chittenden et al. 2010
Annual Mismatch	BIO	Annual survival probability is highest in years where the biological spring transition date occurs before average river exit date for that year.	Cushing 1990, 1969
Annual Mismatch Squared	BIO^2	There is an optimal biological spring transition date, where annual survival probability decreases if peak zooplankton abundance is too early, rises to an optimum coincident with annual average river exit date, and decreases where the biological transition date occurs after average river exit date.	Cushing 1990, 1969
Northern Zooplankton Biomass	Z	Increased biomass of lipid-rich, northern copepods increases survival probability.	Miller et al. 2017; Peterson and Schwing 2003
Size	FL	Larger individual fish have higher survival probability than smaller fish.	Beamish and Mahnken 2001; Ward et al. 1989
Size by River Exit Date	FL^*RE	The effect of river exit date on survival probability is dependent on size, where the effect of river exit date is stronger in smaller fish.	Weitkamp et al. 2015
Size by Year	FL^*Year	The effect of the timing of the biological spring transition date depends on fish size, where annual variation such as changes in the biological spring transition date is less important for larger fish.	Anderson et al. 2013; Litz et al. 2017

fects included a yearly effect of biological spring transition date and the individual-level of the model included size, outmigration timing, northern copepod biomass, the degree of mismatch (strength of the interaction between outmigration date and annual biological spring transition date), and other associated interactions. For the second modelling phase, hereafter the Annual Covariate Inclusion Model, the group-level fixed effects included a yearly effect of one of eleven correlated annual variables (i.e., biological spring transition date, spring upwelling transition date, upwelling strength, air temperature (as a proxy for sea surface temperature), PDO, Aleutian Low Pressure Index (ALPI), ENSO, northern copepod biomass anomaly, southern copepod biomass anomaly, Columbia River discharge and an ecosystem indicator). These are not all the variables that could effect marine survival, as the aim of this study was not to elucidate all factors related to marine survival, but instead to determine if phenological mismatch could be a factor influencing marine survival. The variable selection approach separated the variable selection process from the parameter estimation process of that covariate's effect size to determine which covariates were useful predictors of steelhead trout survival (Royle and Dorazio, 2008).

3.3.1 Wind River steelhead trout

The Wind River steelhead trout population is a wild population in the Lower Columbia River. These fish have a relatively short migration compared to other Columbia River steelhead trout populations, and pass only one hydropower dam. Thus, this population may provide a conservative indicator of smolt-to-adult return rates, with presumably higher survival than more upstream Columbia River populations that have a more perilous downstream migration. Understanding the factors that influence survival of Wind River steelhead trout could help elucidate the factors that affect ocean survival of Columbia River salmon and steelhead trout more broadly. The Wind River is a 582 km^2 watershed located 245 km from the Pacific Ocean on the border of Washington and Oregon, USA (Fig. 3.1). It is composed of three sub-basins, Trout Creek, Panther Creek, and the upper mainstem Wind River, and exits to the Columbia River 15 km upstream from the Bonneville Dam. Shipherd Falls at river kilometer three on the Wind River is a natural barrier to all upstream migrating salmonids, with the exception of summer steelhead trout, which can pass over it. However, some wild steelhead trout, and all hatchery Spring Chinook salmon returning to the Carson National Fish Hatchery, pass upstream of the falls via a fish ladder and trap. Consequently, the only anadromous species in the watershed are wild summer and winter steelhead trout (~200 – 1500 adults and ~8000 – 40,000 smolts) and hatchery spring Chinook salmon. Wind River steelhead trout smolts are mostly summer run, as fewer than ten spawning winter steelhead trout are passed above the falls. The watershed has been managed as a wild steelhead trout gene bank with no hatchery steelhead trout planted in the watershed for the past 20 years. Wind River steelhead smolts are predominantly age-2 (range 1 – 3 years old), with sizes ranging from 78 – 280 mm (Figs. 3.7, 3.8) and migrate to

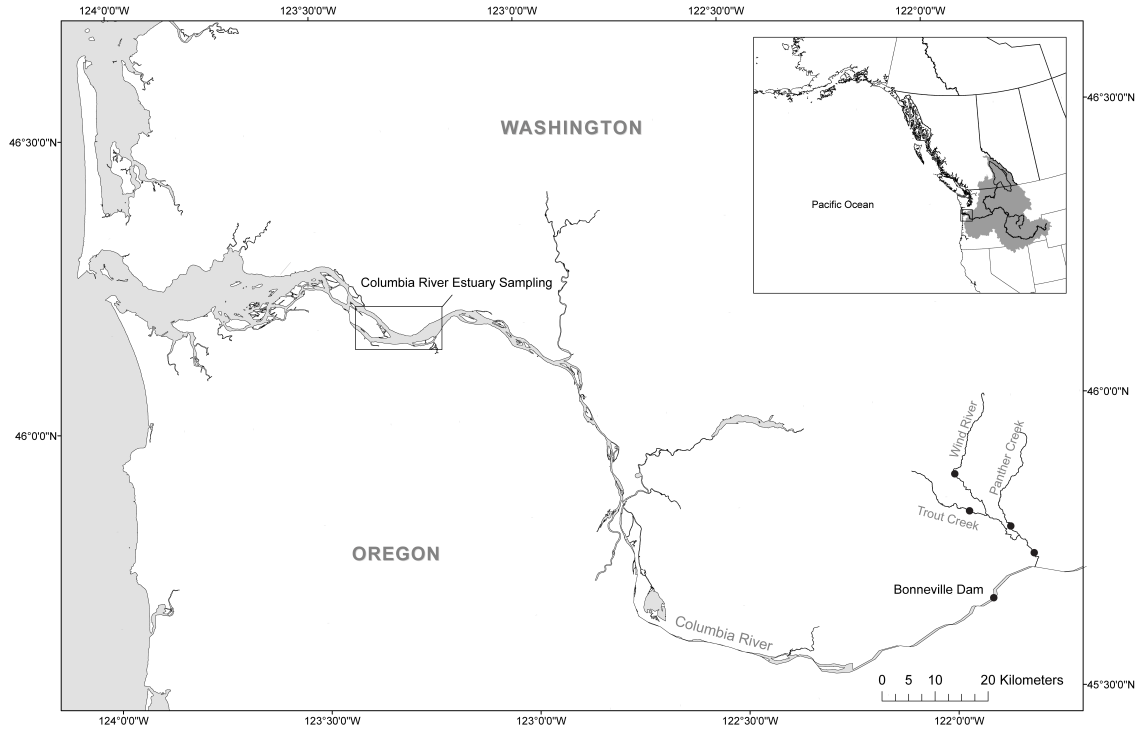

Figure 3.1: Lower Columbia River and the Wind River Basin. There are four rotary screw traps in the Wind River Basin (upper Wind River, lower Wind River, Trout Creek, and Panther Creek), and one set of PIT tag detection arrays at the Bonneville Dam, indicated by black dots. A mobile PIT tag detection array is towed in transects in the Columbia River estuary and the sampled area is indicated by the black box. Zooplankton observation site (NH 05) is located off the map, approximately 200 km south of the Columbia River estuary.

the ocean between early April and late June with an average migration duration of ~11 days (range 2 – 59 days) (Figs. 3.7, 3.9). They spend between ~1 – 3 years in the ocean before returning as adults to spawn (Fig. 3.10). A small percentage of spawning steelhead trout return to the ocean as kelts and may return to freshwater to spawn again in subsequent years. This system has been comprehensively monitored since the 1990s. Beginning in 2003, individual Passive Integrated Transponder (PIT) tagging of juvenile steelhead trout and close to 100% detection at Bonneville Dam fish ladders of adults that survive the ocean stage has enabled analyses linking individual traits (size and outmigration timing) to ocean survival.

Starting in 2003, juvenile steelhead trout were tagged with PIT tags at one of four locations on the Wind River (the upper Wind River, Trout Creek, Panther Creek, and the outlet of the Wind River to the Columbia River; Fig. 3.1) to determine smolt-to-adult return rates as part of a monitoring project led by the Washington Department of Fish and Wildlife. Rotary screw traps were installed annually on or near April 1st and operated until

the end of June in order to capture the end of the juvenile steelhead trout outmigration. Juvenile steelhead trout were captured using a rotary screw trap, anesthetized with MS-222, measured for fork length (FL, in mm), PIT tagged (12 mm tag), and released upstream (1.5 – 6 km) of the trap in which they were captured in order to estimate screw trap capture efficiency. Tag retention and mortality trials were conducted and found minimal tag loss (0.1 – 1%) and short-term tag-related mortality (~1%) (T. Buehrens, unpublished data). Juvenile steelhead trout could be recaptured at several rotary screw traps in the Wind River (the upper Wind River, Trout Creek, Panther Creek, and the outlet of the Wind River to the Columbia River) and detected at downstream static arrays at the Bonneville Dam and at a towed array in the Columbia River estuary. As juveniles, the recapture rate at screw traps and detection efficiency at downstream arrays is low (T. Buehrens, unpublished data), therefore river exit date was the last date that each of the juvenile steelhead trout were detected or the day they were captured as they out-migrated from the Wind River (typically the day they were tagged). We expected that there might be an optimum day of outmigration (either due to phenological synchrony or other environmental factors) and therefore included a river exit date squared term in our model to account for this possibility (see section 3.3.4 Statistical Analyses). Data from PIT tags were obtained from the Pacific States Marine Fisheries Commission (www.ptagis.org).

Survival to adulthood was determined by subsequent detection at the Bonneville Dam as adults. Steelhead trout from the Wind River are protected under the U.S. Endangered Species Act (ESA) and therefore are not targeted for harvest by fisheries below Bonneville Dam. Incidental catch in commercial fisheries is estimated to be less than 2%, based on neighbouring wild steelhead trout populations from the Columbia River (WDFW and ODFW, 2018a,b). Thus, survival was determined by detection at Bonneville Dam, which has a near 100% detection efficiency for PIT tagged adult salmon (Burke et al., 2006). To-date no tagged Wind River adults have been detected upstream without first being detected at Bonneville Dam (T. Buehrens, unpublished data). All returning steelhead trout that were tagged in the Wind River as juveniles returned on their maiden spawning migration (first time spawning) on or before three years in the ocean (Fig. 3.10), therefore we included only juvenile salmon tagged between 2003 and 2014 to allow for up to three years growth in the ocean. We considered a fish to have 'survived' if the fish was detected at Bonneville Dam adult fish ladders more than 330 days after it was tagged and released as a smolt. Fish were considered 'dead' if they were not detected at Bonneville dam by December 31, 2017. Based on this criterion, 22,116 juvenile fish were PIT tagged between 2003 and 2014, and 850 survived and returned as adults (Table 3.2). We used fork length at tagging for size measurement in our analyses and acknowledge that fork length at tagging is only a proxy of fork length at ocean entry as it is likely that fish grew during their 245 km migration downstream.

3.3.2 Zooplankton biomass estimates and biological spring transition date

The coastal shelf of Oregon experiences vernal changes in zooplankton abundance and community composition, resulting in seasonal increases in abundance and quality of salmon prey in coastal environments. In the spring, alongshore wind stress changes from predominantly poleward (downwelling favorable) to predominantly equatorward (upwelling favorable) which reverses coastal currents and results in a shift in the zooplankton community. During the winter, the copepod community is dominated by warm water southern species (e.g., *Mesocalanus tenuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus pergens*, *C. arcuicornis*, and *C. parapergens*, *Calocalanus styliremis*, and *Corycaeus anglicus*), while during the summer, the copepod community is dominated by cold water-affiliated, lipid-rich boreal/northern species (e.g., *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*) (Peterson and Miller, 1977). The timing of this seasonal shift from southern/winter to a boreal/summer copepod community is defined as the biological spring transition date (Peterson and Keister, 2003). The fall transition is signalled by a reversal from predominantly upwelling to downwelling wind stress resulting in the return of the predominantly poleward flowing currents and a return of the southern/winter copepod community. The largest differences in total copepod biomass occur seasonally with copepod biomass peaking during the summer months and decreasing in the winter months (Hooff and Peterson 2006; Fig. 3.2). However, large scale oceanographic patterns such as ENSO or shifts in PDO can also affect the biomass and species composition of zooplankton on inter-annual time scales (Fisher et al., 2015; Keister et al., 2011).

Copepod biomass and the date of the annual biological spring transition were determined from plankton samples collected twice monthly to monthly from a station (NH 05) located on the Newport Hydrographic Line, 9 km off the coast of Newport, Oregon in 60 m water depth (44.65°N, 124.18°W) approximately 200 km south of the Columbia River estuary (for detailed methods see Peterson and Keister 2003). Briefly, zooplankton were collected using a 202 μm mesh size, 0.5 m diameter plankton net towed vertically from near the sea floor to the surface at a rate of 30 m/min. Zooplankton samples were preserved in a 5% buffered formalin/seawater solution and were subsampled with a 1.1 ml Stempel pipette for copepod species identification and enumeration. Density was determined as the number of individuals per m^3 of water sampled and the northern copepod biomass was estimated using length to mass regressions standardized to units of mg C m^{-3} for the cold water taxa (Hooff and Peterson, 2006; Fisher et al., 2015).

The biological spring transition date represents the first day of the year that the northern copepod (zooplankton) community was first reported at NH 05 as defined by cluster analysis (Peterson and Keister, 2003), and obtained by NOAA Northwest Fisheries Science Center (www.nwfsc.noaa.gov/). The match/mismatch hypothesis proposes that there should be an optimum biological spring transition date, which would result in a parabolic relationship

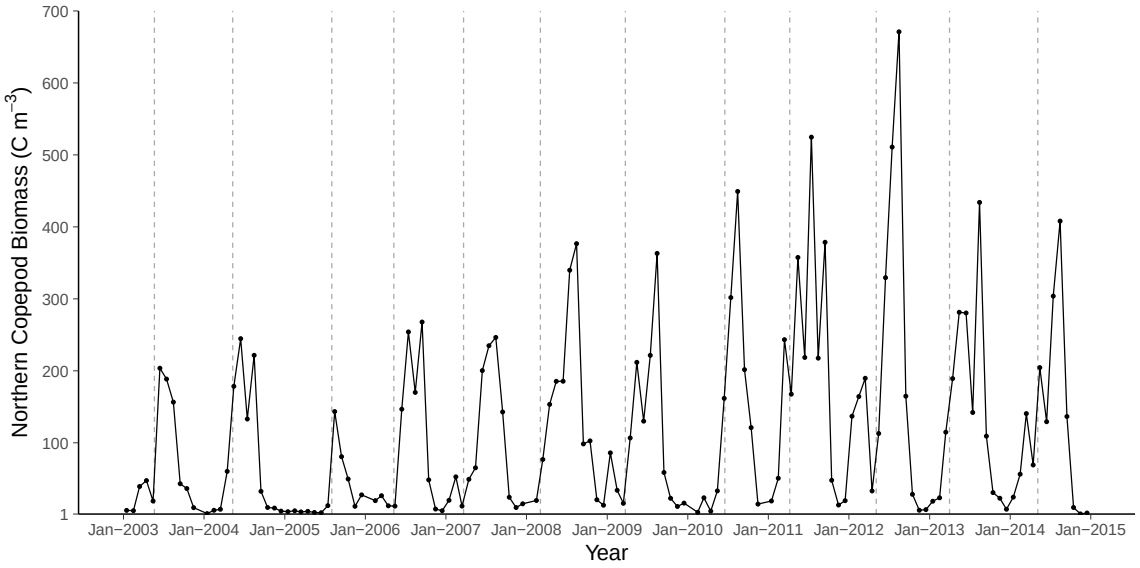

Figure 3.2: Northern copepod biomass between 2003 – 2015 from biweekly to monthly collections off Newport, Oregon (46.5°N). Grey dashed line indicates the biological spring transition date for each year (Peterson and Keister, 2003). Northern/boreal copepod communities are dominated by *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae* (Hooff and Peterson, 2006; Peterson and Miller, 1977).

between biological spring transition date and survival. We therefore calculated a quadratic term (biological spring transition date squared) to account for nonlinearity between the biological spring transition date and survival in our models (see section 3.3.4 Statistical Analyses).

Zooplankton are not a main prey item of juvenile steelhead trout, making up only a small fraction their diet (Daly et al., 2014), yet certain zooplankton species can be used as an index of ocean conditions. Appearance of the northern copepod community in the spring signals a transition to shorter, more energy dense food chains and an ocean ecosystem that is more favourable to the growth and survival of salmonids (Daly et al., 2013; Peterson et al., 2014). In reality, juvenile steelhead trout are likely preying upon euphausiids and icthyoplankton, however conditions favourable to juvenile steelhead trout prey are similar to those favourable to northern copepods (Daly et al., 2014). Therefore, rather than a direct prey resource, we consider northern copepod biomass and the timing of the biological spring transition to be proxies of abundance and timing of ocean conditions favourable to salmon.

In our analyses, biweekly northern copepod species biomass was linked with salmon outmigration date, such that the zooplankton biomass estimate closest to the tagging date of the juvenile steelhead trout was used as the northern zooplankton biomass experienced by that fish. Therefore, each biomass estimate approximates the conditions experienced by individual fish across outmigration dates.

3.3.3 Oceanographic and annual variables

Other oceanic processes that operate at large spatial and temporal scales can also influence ocean survival of steelhead trout. These processes are thought to influence marine productivity through affecting nutrient availability and growing conditions of phytoplankton as well as plankton community composition and energy density (Gargett, 1997). These oceanic processes are correlated with the biological spring transition date and thus are not independent from match/mismatch but could also be important. For example, when PDO is negative the peak in abundance of northern (lipid rich) zooplankton is larger and earlier, and growing season for fish is longer (Keister et al., 2011; Mantua et al., 1997). While it is difficult to untangle these potentially linked processes, it is worth comparing the importance of the mismatch variable (biological spring transition date) in the context of these large-scale oceanic processes. We therefore completed a separate analysis on annual survival data (Annual Covariate Inclusion Model) comparing models including each of these processes, with a degree of mismatch model to determine whether mismatch or these other large-scale correlated variables were most strongly related to ocean survival.

Potential climate variables that are known to influence zooplankton dynamics were collated from existing databases for the years 2003 – 2014. We used mean March to June Coastal Upwelling Index as an indicator of upwelling strength at 45°N, 125°W (National Marine Fisheries Science's Pacific Fisheries Environmental Laboratory, (www.cbr.washington.edu/dart/; Bakun 1973 and see Scheuerell et al. 2009). The physical spring transition date was calculated as the date when the cumulative sum of the Coastal Upwelling Index (beginning January 1) switched from decreasing to increasing, indicating a change from downwelling to upwelling (see Satterthwaite et al. 2014). Mean March to June air temperature was used as a proxy of sea surface temperature (SST), as a continuous dataset of SST was not available near the Columbia River estuary for the time period of interest (see Nickelson 1986; Mueter et al. 2002b). We used air temperature data from two NOAA buoy stations; 46029 (46.14°N, 124.49°W) and 46041 (47.35°N, 124.74°W, National Data Buoy Center; www.ndbc.noaa.gov/)). We included mean April to June Columbia River discharge (gauge height, ft) measured at the Bonneville Dam (USGS site 14128870), as discharge/flow rate could affect survival as well as the size of the Columbia River plume and thus feeding opportunities (Burla et al., 2010; Phillips et al., 2017). We also used the mean March to June PDO estimates (Nathan Mantua, http://research.jisao.washington.edu/pdo/), mean April to June ENSO estimates (National Weather Service, www.cpc.ncep.noaa.gov/), and ALPI (http://open.canada.ca/). We also used three measures of the marine ecosystem: northern copepod biomass anomaly, southern copepod biomass anomaly, and a composite metric of 15 ecosystem indicators derived from principal component analysis (PC1 score of physical and biological indicators such as sea surface temperature/salinity, upwelling, deep sea temperature/salinity, southern and northern copepod anomalies, biological spring transition

date, PDO, ENSO, etc.; see Peterson et al. 2014) used to forecast adult spring and fall Chinook and coho salmon returns to the Columbia River (Table 3.6; Peterson et al. 2014).

3.3.4 Statistical analyses

3.3.4.1 Modeling approach

We used Bayesian multilevel regression models to account for the hierarchical nature of our study system with individual-level covariates (e.g., body size) nested within group- and annual-level covariates (e.g., biological spring transition date; Gelman and Hill 2007; Hox et al. 2018). Our multilevel models predicted steelhead trout survival as a function of scaled and centered individual- and annual-level covariates. Specifically, we assumed individual steelhead trout survival ($\Phi_{i,y,s}$) followed a Bernoulli distribution with survival probabilities ($\mu_{i,y,s}$) estimated from a multilevel regression using a logit-link function such that:

$$\Phi_{i,y,s} \sim Bernoulli(\mu_{i,y,s})$$

where $\Phi_{i,y,s}$ was a zero or one indicating whether an individual fish i survived or not. The probability of survival was calculated using the inverse logit transformation of $\mu_{i,y,s}$, where $\mu_{i,y,s}$ was a linear function of individual- i, year- y, and site- s level predictors and interactions.

3.3.4.1.1 Biological Spring Transition Date Model

For the first phase of model selection, the individual level of the model took the form:

$$logit(\mu_{i,y,s}) = \beta_0 + \beta_{FL}FL_i + \beta_{RE}RE_i + \beta_{RE^2}RE_i^2 + \beta_Z Z_i + \beta_{FL^*RE}FL_iRE_i + \beta_{FL^*Y_y}FL_i + \beta_{RE^*Y_y}RE_i + w_{y,s} \quad (3.1)$$

where β_{FL}, β_{RE}, β_{RE^2}, β_Z, and β_{FL^*RE} were individual level predictors of size FL (fork length in mm), river exit date RE (the year-day the smolt left the Wind River), river exit date squared RE^2(representing optimal river exit date), northern zooplankton biomass Z (matched with outmigration date for individuals), and the interaction between size and river exit date, respectively. The model also included cross-level interactions $\beta_{FL^*Y_y}$ and $\beta_{RE^*Y_y}$ which described annual adjustments to the effect of size and river exit date on survival. The annual adjustment to the effect of size on survival was modelled as follows:

$$\beta_{FL^*Y_y} = \beta_{FL^*BIO}BIO_y + \epsilon_y^{year^*FL^*BIO} \quad (3.2)$$

where the annual adjustment to the effect of size was a fixed effect β_{FL^*BIO} of the biological spring transition date BIO each year, and a year-specific random effect $\epsilon^{year^*FL^*BIO}$:

$$\epsilon_y^{year^*FL^*BIO} \sim normal(0, \tau^{year^*FL^*BIO}) \quad (3.3)$$

The annual adjustment to the effect of river exit date on survival was modelled as follows:

$$\beta_{RE^*Y_y} = \beta_{RE^*BIO} BIO_y + \epsilon_y^{year^* RE^* BIO} \tag{3.4}$$

where the annual adjustment to the effect of size was a fixed effect β_{RE^*BIO} of the biological spring transition date BIO each year, and a year-specific random effect $\epsilon^{year^* RE^* BIO}$:

$$\epsilon_y^{year^* RE^* BIO} \sim normal(0, \tau^{year^* RE^* BIO}) \tag{3.5}$$

Finally, the model also included a group-level (year and site) effect $w_{y,s}$, where the group-level model acted as a prior for individual-level year-site specific intercept (Gelman and Hill, 2007):

$$w_{y,s} = \beta_{BIO} BIO_y + \beta_{BIO^2} BIO_y^2 + \epsilon_{y,s}^{year^* s} \tag{3.6}$$

modelled as fixed effects β_{BIO} of the biological spring transition date BIO and β_{BIO^2} of the biological spring transition date squared BIO^2 (representing optimal timing of spring productivity) for each year, and a nested random effect of site within year:

$$\epsilon_{y,s}^{year^* s} \sim normal(\epsilon_y^{year}, \tau_{site}) \tag{3.7}$$

based on a global (across sites) random effect of year:

$$\epsilon_y^{year} \sim normal(0, \tau_{year}) \tag{3.8}$$

We used Bayesian variable selection to determine the probability that a parameter occurred in the best model, which consequently provided an intrinsic estimate of parameter importance. In Bayesian variable selection each variable $X_{i,j}$ is multiplied by a Bernoulli distributed inclusion probability ω with prior probabilities of 0.5 (Hooten and Hobbs, 2015; Royle and Dorazio, 2008) such that:

$$logit(\mu_{i,y,s}) = \beta_0 + \omega \beta_1 X_{i,y} + \epsilon_{y,s} \tag{3.9}$$

Thus, as the posterior probability of the inclusion variable approaches 0 or 1, certainty that the variable is to be excluded or included, respectively, increases. Conversely, a posterior probability of 0.5 (i.e., the effect of a covariate was as likely as a fair coin flip) demonstrates uncertainty as to whether the variable should be included or not. For variables that included

interactions, including quadratic terms, probability of inclusion was adjusted from 0.5 based on the probability of higher-level terms occurring. Thus, the probability of the base term(s) (e.g., x, x_1, x_2) occurring depended on the probability of the higher level term (e.g., x^2, $x_1 \cdot x_2$) occurring (Hooten and Hobbs, 2015; Kruschke, 2015; Kuo and Mallick, 1998).

$$\omega_1 = Bernoulli(p_1) \tag{3.10}$$

$$p_1 = \omega_2 + (1 - \omega_2 0.5) \tag{3.11}$$

$$\omega_2 = Bernoulli(p_2) \tag{3.12}$$

The probability of inclusion of the base term ω_1 was either a 0 or 1 based on the mean of the Bernoulli distribution p_1, where p_1 is dependent on the probability of the higher-level interaction occurring. The variable inclusion probability of the higher-level interaction occurring ω_2 was either 0 or 1, given by a Bernoulli distribution with a mean of $p_2 = 0.5$. In the case where the interaction involved a categorical variable, p_2 is the average inclusion probability for each interaction parameter, rather than 0.5. For example, for the interaction between year and size there are twelve parameters (one for each year); a parameter inclusion variable was assigned to each of the twelve parameters and the average of all twelve inclusion parameters was used as p_2 (Kuo and Mallick, 1998). Inclusion probabilities were estimated for all individual-level fixed effects (β_{FL}, β_{RE}, β_{RE^2}, β_Z, and β_{FL^*RE}), cross-level interactions ($\beta_{FL^*Y_y}$, $\beta_{RE^*Y_y}$), and group-level fixed effects (β_{BIO}, β_{BIO^2}). Parameter estimates in models employing Bayesian variable selection are intrinsically model-averaged (Kuo and Mallick, 1998; Royle and Dorazio, 2008; Hooten and Hobbs, 2015). Parameters with inclusion probabilities greater than 0.5 were considered to be included in the best model(s).

3.3.4.1.2 Annual Covariate Inclusion Model

For the second phase of our model selection, the Annual Covariate Inclusion Model, we simplified the individual level of the model to include only covariates that had greater than 50% inclusion probability in the Biological Spring Transition Date Model, and instead tested the annual covariates. The individual level of the Annual Covariate Inclusion Model took the form:

$$logit(\mu_{i,y,s}) = \beta_0 + \beta_{FL} FL_i + \beta_{RE} RE_i + \beta_{RE^2} RE_i^2 + \beta_{RE^*Y_y} RE_i + w_{y,s} \tag{3.13}$$

The annual adjustment to the effect of river exit date on survival was modelled the same as the Biological Spring Transition Date Model (Equation 3.4, Equation 3.5). Similarly, this model included a group-level (year and site) effect $w_{y,s}$, which functioned as a prior for individual-level year-site specific intercept (Gelman and Hill, 2007).

$$w_{y,s} = \beta_A A_y + \epsilon_{y,s}^{year^* s} \tag{3.14}$$

where β_A is a fixed effect of the one of the annual covariates A_y for each year and a nested random effect of site within year (Equation 3.7), based on a global (across sites) random effect of year (Equation 3.8).

In the Annual Covariate Inclusion Model we used a different Bayesian variable selection approach to determine the probability that an annual parameter should be included in the model. Most annual predictors were highly correlated (Fig. 3.15) and thus inclusion of multiple annual predictors would violate the underlying assumptions of linear models. Therefore, we used a categorical predictor variable with a Dirichlet probability distribution to select one of 11 annual covariates for inclusion in the model:

$$A_y = \begin{cases} A_{1,y}| & \delta_y = 1 \\ A_{2,y}| & \delta_y = 2 \\ & ... \\ A_{11,y}| & \delta_y = 11 \end{cases} \tag{3.15}$$

$$\delta_y = categorical\left(\frac{\rho_{nt}}{\sum_{n=1}^{11}\rho_{nt}}\right) \tag{3.16}$$

where δ_y was an indicator variable (see Table 3.6 for variable assignment). Each annual indicator had a prior of ρ_t= 1/11.

3.3.4.2 Priors

We used vague priors in order to allow the likelihoods to dominate the priors in determining the posterior. Fixed effects (all β's) were given normal priors with a mean of zero (since our data were scaled and centered), and standard deviation of one or three. The precision parameters (all τ's) were given gamma priors with shape and rate parameters of 0.01. We ran our Biological Spring Transition Date Model with fixed effect priors that had a standard deviation of one or three, since inclusion probability can be strongly influenced by prior variance (Kruschke, 2015). Models fit with parameter priors that were assigned standard deviations of one and three produced similar results, demonstrating our variable selection was robust to changes in standard deviation. We report on the model with the normally distributed priors with mean of zero and standard deviation of one. Fixed effect priors for the Annual Covariate Inclusion Model had a mean of zero and a standard deviation of one.

3.3.4.3 Model fitting and diagnostics

Our models were fitted in the R statistical computing environment (R Core Team 2018) with GUI RStudio (v1.1.423, 2018) using JAGS and `rjags` (Plummer, 2018) and `runjags` packages (Denwood, 2017). Our models used six MCMC chains with 350,000 iterations. A

burn in of 100,000 iterations of each chain was used and the chains thinned at a rate of 1:100, resulting in 2,500 samples retained per chain. JAGS code for both models can be found in Section 3.7.3 of the Supplementary Methods. Starting values were jittered for each chain. We verified chain mixing visually using trace plots and a Gelman-Rubin diagnostic test on each parameter to confirm convergence Rhat <1.1. We then used graphical posterior predictive checks of predicted vs. observed survival probability for each year (Figs. 3.11, 3.16). We checked all covariates for evidence of correlation since inclusion probability can be sensitive to correlations among covariates. None of our sub-annual covariates were correlated, with the highest correlation being 6%.

3.4 Results

Using a dataset of 22,116 juvenile steelhead trout PIT tagged between 2003 and 2014, we investigated patterns of individual and annual ocean survival of steelhead trout (Table 3.2). Annual smolt-to-adult survival rates varied from 1.8% to 7.6% and averaged 4%. Smolt size, while variable across individuals within a year, was relatively consistent across years and had no pattern throughout the outmigration period (i.e., larger fish did not emigrate first; Fig. 3.7). Similarly, average river exit date was also relatively consistent from year to year, but there was substantial within-year variation—about 50 days separated the 5% from the 95% migrant. In contrast, the timing of the biological spring transition date was extremely variable from year-to-year during this time series, with a range of 151 days. The earliest biological spring transition dates occurred in early March and corresponded with some of the highest annual smolt-to-adult survival rates observed in the dataset, while late biological spring transition dates in July and August resulted in among the lowest smolt-to-adult survival rates (Table 3.2, Figs. 3.3, 3.13).

3.4.1 Biological Spring Transition Date Model

We compared Biological Spring Transition Date Model fit and variable importance of multilevel models fit with individual and annual variables and associated interactions to determine which variables correlated with ocean survival of steelhead trout. The variables most likely to be included in the top model were size (FL; 100%), river exit date (RE; 99%), river exit date squared (RE^2; 96%), river exit date and year interaction (RE^*Year; 91%), and biological spring transition date (BIO; 64%) (Table 3.3). Parameter estimates show that survival was positively associated with individual size, and negatively associated with the annual biological spring transition date (Fig. 3.4). We found evidence of an optimal outmigration date (Figs. 3.4, 3.5), and this optimum varied among years (Fig. 3.6). The most probable model included size, river exit date, river exit date squared, the biological spring transition date, and an interaction between river exit date and year (33%; Table 3.4).

Table 3.2: Mean annual values for mismatch variables and smolt-to-adult return rates.

Year	Biological Spring Transition Date	River Exit Date (range)	Mean FL (range)	Smolt-to-Adult Returns (survivors/total)
2003	21-May	May 7 (Apr 11 – Jun 13)	164 (122, 256)	0.029 (39, 1343)
2004	10-May	May 2 (Mar 31 – Jun 7)	164 (114, 258)	0.022 (47, 2105)
2005	02-Aug	May 3 (Apr 4 – Jun 6)	163 (122, 255)	0.018 (38, 2097)
2006	10-May	May 11 (Mar 30 – Jun 12)	162 (120, 226)	0.037 (48, 1298)
2007	22-Mar	May 3 (Apr 3 – Jun 8)	162 (102, 280)	0.058 (158, 2741)
2008	04-Mar	May 10 (Apr 4 – Jun 29)	160 (125, 238)	0.070 (81, 1155)
2009	24-Mar	May 7 (Apr 5 – Jun 11)	163 (125, 215)	0.076 (102, 1346)
2010	18-Jun	May 14 (Apr 5 – Jun 2)	161 (120, 237)	0.044 (89, 2006)
2011	08-Apr	May 14 (Apr 9 – Jun 27)	159 (120, 215)	0.018 (25, 1404)
2012	04-May	May 15 (Apr 14 – Jun 26)	158 (130, 239)	0.035 (41, 1159)
2013	06-May	May 9 (Apr 2 – Jun 21)	161 (90, 227)	0.039 (103, 2613)
2014	06-May	May 4 (Apr 5 – Jun 8)	159 (78, 234)	0.028 (79, 2849)

Biological spring transition date was the first day of the year that cold water zooplankton were detected at NH 05. Remaining columns are mean river exit date, fork length (FL, in mm), and smolt-to-adult returns as a proportion of survivors over total number tagged.

Survival varied throughout the outmigration period, rising to an optimum, that varied across years. Three of the four terms that included river exit date (RE, RE^2, RE^*Year) had inclusion probabilities greater than 91%. However, 95% credible intervals of the parameter estimate for river exit date were highly uncertain and spanned zero (mean β_{RE}= -0.12, 95% CI = -0.32 – 0.07; Fig. 3.4; Table 3.7), where reported parameter values are model-averaged estimates. This indicates that river exit date is an important predictor of survival but that the size of the effect was uncertain. There was clear evidence for an optimal outmigration date as average survival probability across all years in the dataset increased from <2% survival around April 1st, reaching an optima of 3% survival around May 1st, and decreased throughout the remainder of the outmigration period reaching a low of <0.5% on June 30th (mean β_{RE^2}= -0.13, 95% CI = -0.19 – -0.06; Figs. 3.4; 3.5; Table 3.7). Importantly, the relationship between river exit date and survival differed across years—optimal river exit timing varied annually. Inclusion probability of the interaction between river exit date and year was high (91%), and strength of the effect differed by year (Fig. 3.4). However, there was no clear pattern between river exit date optima and the annual biological spring transition date (R^2=0.01, Fig. 3.14). This suggests that while inter-annual outmigration timing is likely an important predictor of survival, factors other than just annual biological spring transition date seem to control inter-annual variation in optimal river exit.

Table 3.3: Variable inclusion probability of terms predicting ocean survival of steelhead smolts for the Biological Spring Transition Date Model.

Variable	Variable Inclusion Probability
FL	**1.000**
RE	0.993
***RE*^{2}**	**0.963**
RE^*Year	0.907
BIO	**0.639**
***RE**FL**	**0.209**
Z	0.089
BIO^2	0.087
FL^*Year	0.078

Variables include river exit date (RE), fork length (FL), total zooplankton biomass (Z), biological spring transition date (BIO). (*) indicates an interaction term. The RE^*Year interaction is the intra-annual mismatch term. Terms that have credible intervals that do not cross zero are bolded.

Years with earlier biological spring transition dates had higher marine survival of steelhead trout. Survival was strongly and negatively related to the biological spring transition date (mean β_{BIO} = -0.39, 95% CI = -0.70 – -0.07; Table 3.7) and this variable had one

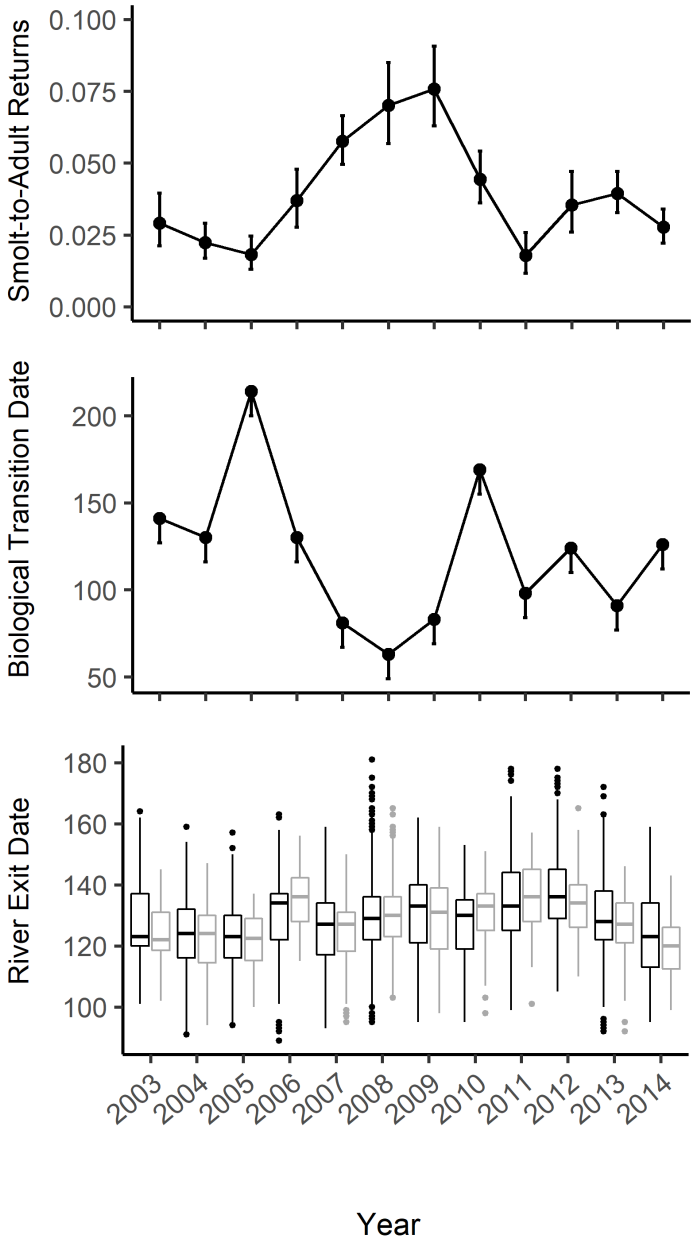

Figure 3.3: Yearly smolt-to-adult return (SAR) rates (top), biological spring transition date, which is the first day cold water zooplankton were found off the coast of Newport, OR (middle) and year-day of river exit (boxplots with the 25^{th}, median, and 75^{th} percentiles) and fate (survivors (light grey) and deaths (black); bottom) for smolt ocean entry years 2003 – 2014.

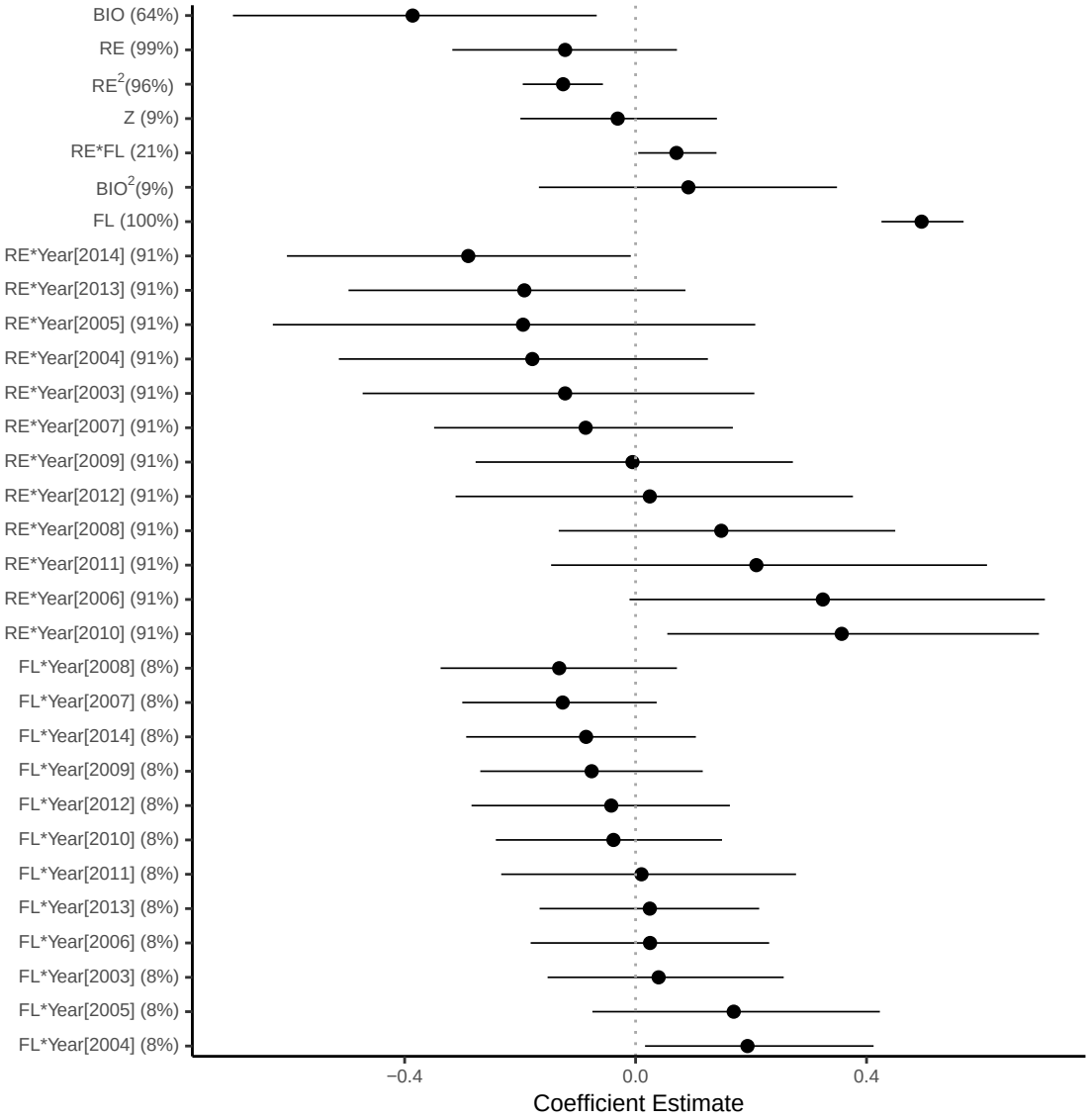

Figure 3.4: Coefficients for terms in the Biological Spring Transition Date Model. Black point is the mean, and lines are the 95% credible intervals. Variables include river exit date (RE), fork length (FL), northern copepod biomass (Z), biological spring transition date (BIO). (*) indicates and interaction term. Percent in brackets beside each term indicates the variable inclusion probability for that term (Table 3.3).

Table 3.4: Top ten candidate model performance for predicting survival of individual steelhead trout.

Variable	Variable Inclusion Probability
$FL + RE + RE^2 + RE^*Year + BIO$	0.325
$FL + RE + RE^2 + RE^*Year$	0.218
$FL + RE + RE^2 + RE^*Year + BIO + FL^*RE$	0.086
$FL + RE + RE^2 + RE^*Year + FL^*RE$	0.057
$FL + RE + RE^2 + RE^*Year + BIO + BIO^2$	0.049
$FL + RE + RE^2 + RE^*Year + BIO + zooplankton\ biomass$	0.035
$FL + RE + RE^2 + BIO$	0.031
$FL + RE + RE^2 + RE^*Year + BIO + FL^*Year$	0.022
$FL + RE + RE^2 + RE^*Year + zooplankton\ biomass$	0.018
$FL + RE + RE^2$	0.017
$FL + RE + RE^2 + RE^*Year + FL^*Year$	0.014
$FL + RE + RE^2 + RE^*Year + BIO + BIO^2 + FL^*RE$	0.014

Variables include river exit date (RE), fork length (FL), total zooplankton biomass (Z), biological spring transition date (BIO). (*) indicates an interaction term. The RE^*Year interaction is the intra-annual mismatch term.

of the largest effect sizes of all parameters (-0.39 compared to 0.50 for size; Fig. 3.4). For example, an average-sized fish (160 mm) migrating during peak outmigration in a year where the biological spring transition date occurred ~March 22nd (1 SD before the mean biological spring transition date) had 1.5 – 2 times higher probability of survival (4.3%) than it would if it migrated in a year when the biological spring transition date occurred on June 12th (2.6%; 1 SD after the mean biological spring transition date; Fig. 3.5). Thus, there was partial support for the annual mismatch hypothesis. On the one hand, there was little evidence for an optimum biological spring transition date (9% inclusion probability of the quadratic term, Table 3.3), indicating a linear relationship where earlier biological spring transition dates were related to higher survival. Yet, annual patterns of the timing of energy-rich (northern) zooplankton availability appear related to annual smolt-to-adult survival rates.

Larger than average individuals had a higher probability of survival than smaller individuals. In the Wind River, average marine survival of steelhead trout larger than 177 mm (1 SD larger than the mean) was 2.5 times higher than a fish of 146 mm (1 SD below the mean; Fig. 3.5). The benefit of large body size was consistent regardless of outmigration date as evidence by the low inclusion probability (20%, Table 3.3) for the interaction between size and river exit date, (mean $\beta_{FL^*RE} = 0.07$, 95% CI = 0.01– 0.14; Fig. 3.4; Table 3.7). Body size also did not interact with year, suggesting no year-specific size-dependent relationship (inclusion probability of 8%). The year intercept included the biological spring transition date, and a random effect, where biological spring transition date explained 41% of yearly

variation in survival. Northern copepod biomass was included in only 9% of models. The effect size was small and overlapped zero (mean β_z= -0.03, 95% CI = -0.20 – 0.14; Table 3.7), indicating a lack of association with survival (Table 3.3). Finally, site was included as a random effect nested with year to account for the differences in survival between fish tagged in different locations within the watershed, however, coefficients for the random effect of site varied little between sites.

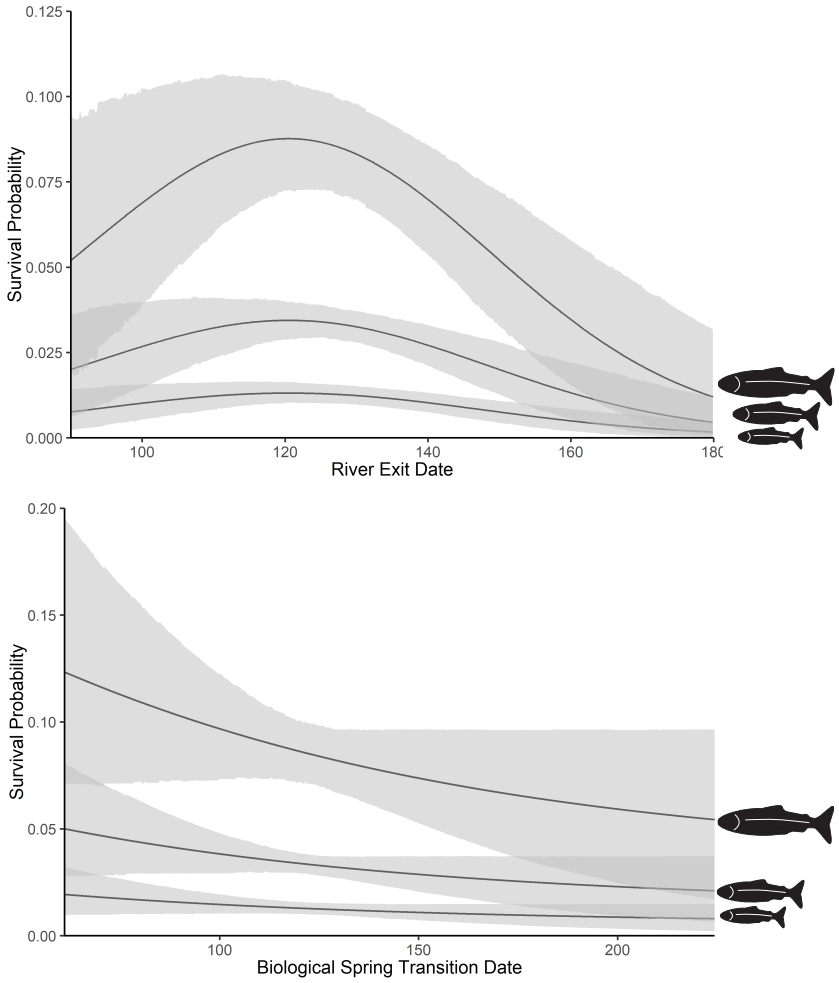

Figure 3.5: Posterior predictions of survival probability for Wind River juvenile steelhead trout at the mean and ±2 SD of observed sizes (130 mm, 160 mm, 192 mm) across the observed time lags (top) and biological spring transition date (bottom) using model averaged coefficients (Table 3.3, Fig. 3.4). Shaded area indicates 95% high probability density interval. Predictions are based on other terms at their mean, and variable weighting based on variable inclusion probability.

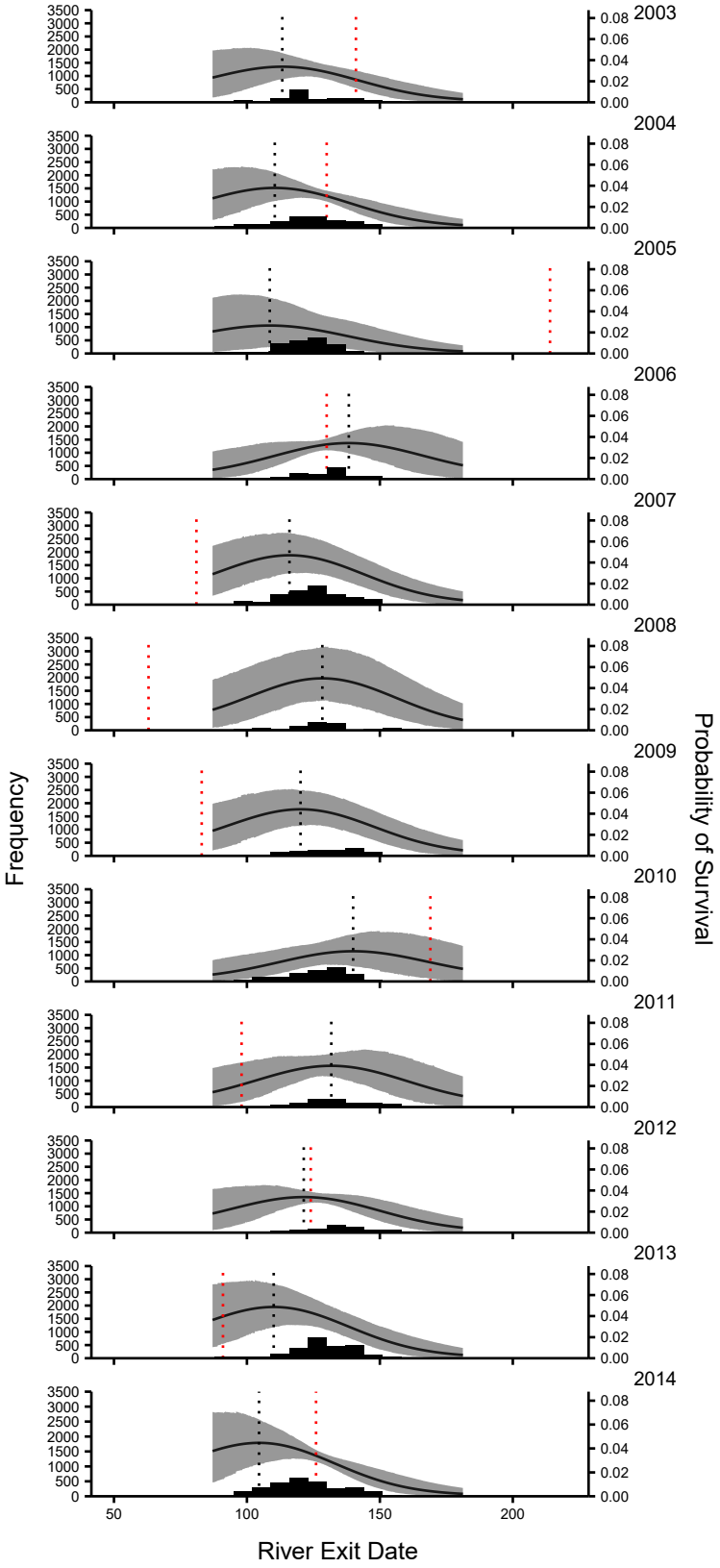

Figure 3.6: Effect of the degree of mismatch on model predictions of survival probability for river exit date for each year. The river exit date by year interaction represents the individual-level match/mismatch term. Solid bars represent daily smolt outmigration frequency. Solid black line indicates mean probability of survival with shaded area indicating 95% high probability density interval. Vertical red line indicates biological spring transition date and dotted black line indicates optimal river exit date for that year. Predictions are based on other terms at their mean, and variable weighting based on variable inclusion probability.

3.4.2 Annual Covariate Inclusion Model

Of the eleven annual-level variables evaluated for their potential association with survival, we found that four had inclusion probabilities above 9% (the cut off for variable importance is determined by the number of variables being compared – in this case 11 variables means the cut off is 1/11, or 9%). Air temperature off the coast of Washington, USA, was the best predictor with an inclusion probability of 52.7%, followed by the timing of the spring upwelling transition date off the coast of Washington (16.8%), PDO (12.2%) and finally ecosystem indicator (10.4%; Table 3.5). Biological spring transition date had a lower variable inclusion probability (2.6%) but had credible intervals that did not cross zero (mean β_{A_1} = -0.32, 95% CI = -0.60 – -0.02; Table 3.8), indicating a large, but uncertain effect size.

Table 3.5: Variable inclusion probability of terms predicting ocean survival of steelhead smolts for the Annual Covariate Inclusion Model.

Variable	Variable Inclusion Probability
Sea Surface Temperature	0.527
Spring Upwelling Transition Date	0.168
PDO	**0.122**
Ecosystem Indicators	**0.104**
Biological Spring Transition Date	**0.026**
Southern Copepod Index	0.019
Upwelling Strength	0.011
ENSO	0.007
Columbia River Discharge	0.007
ALPI	0.006
Northern Copepod Index	0.005

Variables include Aleutian Low Pressure Index (ALPI), Pacific Decadal Oscillation (PDO), El Niño Southern Oscillation (ENSO). Terms that have variable inclusion probabilities higher than 0.09 were included in model averaging. Terms than have credible intervals that do not cross zero are bolded.

3.5 Discussion

Here we examined individual and annual survival of greater than 22,000 juvenile steelhead trout over a decade of research. Our study had two key findings. First, at the individual level, survival was strongly size- and timing- dependent: larger fish had higher survival and optimal river exit date varied across years. Optimal individual outmigration timing varied within and across years, but this variation was poorly explained by biological spring transition date. Second, across years, survival was higher in years when the biological spring transition date occurred earlier in the year and before Wind River smolt outmigration (Fig. 3.5). This increased survival also corresponded to earlier spring upwelling transition dates

and cooler sea surface temperatures off of coastal Washington. Therefore, we found partial support for both annual and inter-annual mismatch hypothesis (Table 3.1). Marine survival was dramatically lower in years when the biological spring transition date occurred after smolt outmigration, suggesting that when estuaries and coastal environments have low quality prey/growing conditions when outmigration occurs, marine survival is much lower, compared to years when high quality lipid rich prey is present throughout smolt outmigration. Collectively, our study provides evidence that outmigration year-class strength can be determined by shared conditions experienced during early ocean phase as well as key population traits of size and river exit date governed by freshwater growing conditions.

Survival was related to outmigration timing, and the optimum outmigration timing varied from year to year. We predicted that outmigration timing would influence the survival of outmigrants (Table 3.1). Outmigration timing was an important variable for predicting survival, and there was strong evidence for an optimal river exit date. On average, survival probability peaked 7 – 10 days before peak outmigration timing. While we specifically predicted that the optimal river exit date would be related to the annual biological spring transition date, this was not the case. Instead, annual phenological factors in the estuary or ocean other than annual biological spring transition date appeared to be associated with optimal river exit date (Fig. 3.6).

Freshwater growing and migration conditions may also influence inter-annual variation in optimal river exit date. For example, Wind River steelhead smolts migrate for different lengths of time which could represent significant additional unexplained variation in outmigration timing (Figs. 3.7; 3.9). Approximately 10% of tagged smolts were subsequently detected downstream 2 – 59 (median 8) days after tagging at either the Bonneville Dam or in the Columbia River estuary. The range in outmigration dates within a year generally spanned 60 days, so differences in migration rates could have modified the window of arrival in the estuary. Therefore, it is possible that any potential relationship between river exit date and biological spring transition date was confounded by differing migration rates.

There was strong evidence that inter-annual timing of prey availability was an important predictor of survival, yet the findings did not conform to the classic match/mismatch hypothesis. Cushing's original match/mismatch hypothesis proposed that both predators and prey are temporally pulsed (i.e., are present in large number for a short period of time within the year), and peak synchrony would result in the highest recruitment (Cushing, 1990, 1969). Based on our annual mismatch hypothesis, we predicted that biological spring transition date would be an important variable in explaining annual patterns in smolt-to-adult survival. Biological spring transition date varied widely across years ranging between March 4th and Aug 2nd (~150 days) whereas average outmigration date did not appear to vary substantially throughout the monitored period (2003 – 2014; Fig. 3.3). Thus, annual changes in biological spring transition date represent annual changes in phenological mismatch. However, we found limited evidence for a biological spring transition date that

optimized survival, and instead discovered that steelhead trout survival was higher if the biological spring transition date occurred earlier in the year. The transition from a winter to a summer copepod community occurs rapidly and is marked by a drastic increase in zooplankton biomass. Although steelhead trout migration occurs over approximately two months in this system, the window of optimal prey can easily be missed, if outmigration occurs prior to the onset of the lipid rich copepod community following the biological spring transition (Fig. 3.2). Thus, rather than a small window of optimal outmigration timing as predicted by the match/mismatch hypothesis, it appeared that survival increases as biological spring transition date gets earlier in this system, at least within the range of observed transition dates in our short time series. The timing of the biological spring transition date is an index of when energy-rich northern copepods become available to higher trophic levels including larval fish and mesozooplankton. Though copepods are not the dominant prey of juvenile steelhead trout, they are a proxy of good or poor ocean conditions for salmon (Miller et al., 2017). While biological spring transition date was important in our model, it explains only 41% of the yearly variation, and it is likely that other shared freshwater or marine conditions impacted survival. Indeed, results from our Annual Covariate Inclusion Model show that sea surface temperature and spring upwelling transition date were important predictors of steelhead marine survival. Interestingly, both of these variables could be related to growing/feeding conditions in regions north of the Columbia River, where steelhead trout are thought to migrate to quickly and feed (Daly et al., 2014; McMichael et al., 2013; Rechisky et al., 2012, 2009; Van Doornik et al., 2019). This evidence supports the annual mismatch hypothesis but suggests that marine regions to the north are likely more important for steelhead survival than the Columbia River estuary.

Another possible reason survival is not optimal at a phenological match is that Wind River steelhead trout smolts are larger than other anadromous salmon species and are partly piscivorous by the time they leave their natal rivers (Daly et al., 2014; Myers, 2018). Indeed, steelhead trout are unlikely to eat copepods, but rather we used copepods as an indicator of food web quality, such that in years where the biological spring transition date is earlier, there could be more larval fish in the late spring (Daly et al., 2014). Additionally, the species composition and abundance of larval fish during the winter (Jan to Mar) are good indicators of the future prey available to outmigrating salmon (Daly et al., 2013). Larval fish abundance has been related to juvenile salmon survival and might also be a good indicator of future prey available to outmigrating Wind River steelhead trout smolts. Further analysis into the timing and abundance of larval fish could be an interesting avenue of future salmon mismatch studies. Regardless, our findings add important biological realities to the classic match/mismatch hypothesis, and reveal that when high quality prey are available during ocean entrance, survival of Wind River steelhead trout is higher.

Other studies have found that timing of prey availability matters for salmon. Scheuerell et al. (2009) found similar results to our study using individually tagged Snake River Chi-

nook salmon and steelhead trout. Individuals leaving earlier in the year had higher survival than those leaving later in the year. They found a significant interaction between exit date and year that was not related to spring upwelling date. They did not find evidence that upwelling date affected survival, but noted a small sample of only four years was not enough to examine inter-annual variability. On the other hand, a time lag of 70 – 115 days from the spring upwelling transition date produced an optimal survival probability for hatchery-reared Chinook salmon from the California Valley (Ryding and Skalski, 1999; Satterthwaite et al., 2014). Relationships between smolt migration timing and annual timing of spring productivity have been found in some populations of pink salmon, where an early spring phytoplankton bloom benefited northern populations. However, these trends were reversed for southern pink salmon populations such as those in southern British Columbia, where later phytoplankton blooms were shown to increase productivity in pink salmon (Malick et al., 2015a; Mueter et al., 2002a). Interestingly, in our study, northern copepod biomass was not strongly correlated with survival, despite evidence that food availability can affect ocean survival (Peterson and Schwing, 2003; Ruggerone and Goetz, 2004; Tanasichuk and Routledge, 2011). Availability of food during the first 45 days in the ocean correlated with sockeye salmon survival in British Columbia (Tanasichuk and Routledge, 2011). Increased food availability shifted the onset of piscivory to be earlier, where an earlier shift to piscivory was correlated with increased growth and survival in subyearling Chinook salmon (Litz et al., 2017). Thus, our study adds to the growing body of evidence that the phenology of nearshore marine prey can influence marine survival in salmon, but the strength of this correlation is likely dependent on species and food web structure (Durant et al., 2005).

Intra-annual variability in outmigration timing likely acts as a buffer that stabilizes populations in the face of unpredictable and highly variable ocean conditions. Outmigration periods for Wind River steelhead trout were broad, ranging more than 60 days. Additionally, migration rates appeared to vary highly among the subset of fish tracked to Bonneville Dam and the Columbia River estuary, ranging from 2 – 59 days. Interestingly, few late migrating fish took longer than 30 days to complete their freshwater migration resulting in later fish having less variable and faster migration rates, compared to fish leaving the Wind River at the beginning of their migration (Fig. 3.7). Together, the window of ocean-entry by Wind River fish likely varies by more than three months. This breadth in phenological expression may function as a bet-hedging strategy that would in effect protect populations from variability in ocean conditions that are difficult or impossible to predict based on local environmental cues (Beamish et al., 2013; Carr-Harris et al., 2018; Freshwater et al., 2019; Schindler, 2019). Indeed, the optimal date of migration varied across years by ~35 days. Within large river systems, different salmon populations have different outmigration timing, and this may further stabilise the metapopulation from extreme swings in ocean conditions (Beamish et al., 2016; Carr-Harris et al., 2018; Sturrock et al., 2019). Here we provide critical empirical support for the hypothesis that breadth in migration timing is

a key life-history trait that provides resilience to populations faced with variable ocean climates.

Larger steelhead trout had higher marine survival compared to smaller fish, when all other variables were equal. Thus, marine survival is not just related to oceanic conditions, but also characteristics carried over from freshwater. We found that size at river exit was more important than timing of food availability, where larger fish have higher ocean survival, irrespective of timing of the biological spring transition date. Previous studies have also found that larger than average salmon smolts may have higher ocean survival (Beacham et al., 2014a; Beamish and Mahnken, 2001; Ward et al., 1989), but not always (Anderson, 1988; Beamish et al., 2010; Ulaski et al., 2020). Given that hatchery steelhead smolts are larger than wild steelhead smolts, our results could be interpreted as suggesting that hatchery smolts would have higher survival. However, we suggest caution when applying our results to hatchery fish as hatchery fish may respond differently to shared environmental conditions compared to wild fish, and generally have much lower survival probability (Jonsson et al., 2003). Furthermore, size-at-age may be an important factor determining marine survival, however age data were not available (Ulaski et al., 2020). A diversity of freshwater factors may control steelhead trout smolt size, ranging from species interactions with co-occurring salmon to weather and density dependence (Bailey et al., 2018); our results indicate that these factors can have carryover effects on marine survival.

Our results are particularly important given increased variability in ocean conditions and increased prevalence of anomalous warming events. Climate change is warming sea surface temperatures and advancing zooplankton biomass peaks globally, but not all species are advancing at the same rate (Richardson, 2008). Our model results suggest that phenological shifts towards ocean conditions favorable for an earlier onset of a lipid rich zooplankton community could be beneficial for steelhead trout in this region. However, warm ocean conditions favor a delayed, or non-existent, shift to a lipid rich zooplankton community (Peterson et al., 2017). Low frequency warming events associated with the PDO and ENSO have modified the zooplankton community in the northern California Current, resulting in copepod communities dominated by lipid poor subtropical species (Keister et al., 2011; Fisher et al., 2015). A recent anomalous event, coined 'the Blob', first impacted the northern California Current in the fall of 2014 and lasted at least through 2016. This event had far-reaching effects on the northeastern Pacific pelagic ecosystem (Auth et al., 2018; Peterson et al., 2017). This anomalous event resulted in a lack of a biological spring transition in 2015 and 2016, the two years after our study, such that the copepod community remained a lipid-depleted community, which had only been recorded once before in the 22-year time series during the strong El Niño in 1997/98. For example, smolt-to-adult returns for smolts migrating in 2015 were 1.0%, the lowest in the history of the Wind River steelhead trout monitoring project (Buehrens and Cochran, 2018). If 2015/16 years are any indication of future ocean conditions under increasing climate pressure, increased biomass of less nutritious

zooplankton are unlikely to be beneficial to steelhead trout. More broadly, the outmigration timing of some salmon species appears to be lagging behind advancement of regional phytoplankton blooms and it is unclear what effect, if any, this will have on salmon population dynamics (Kovach et al., 2013; Otero et al., 2014; Taylor, 2007). Based on our findings, climate-induced shifts in phytoplankton blooms could affect salmon survival insofar as they affect zooplankton community composition and timing of peak biomass of lipid-rich zooplankton species. Indeed, other studies have found that shifts in the zooplankton community composition and abundance can affect the survival of salmon (Peterson and Schwing, 2003). Further investigation of the effect of food quality vs. timing on salmon survival would be an interesting and relevant avenue for future research.

There is overwhelming evidence that bottom-up processes influence anadromous salmon and trout survival, but that does not preclude other factors such as competition and predation from being major contributors to early ocean survival (Pearcy, 1992). For example, Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritis*) occupying dredge spoil islands in the Columbia River estuary consumed between 10 – 20% of steelhead trout smolts leaving the Columbia River from 2008 – 2013 (Hostetter et al., 2015). In another example, increases in harbour seal (*Phoca vitulina*) populations have been correlated with decreases in wild Fraser River Chinook salmon (Nelson et al., 2019). Top-down pressure from predation can be size-biased, and is a likely contributor of variation in early marine survival, which is not directly accounted for by our model or the match/mismatch hypothesis (Emmett et al., 2006; Osterback et al., 2013; Roby et al., 2003; Tanasichuk and Emmonds, 2016). However, faster somatic growth rates that occur during a phenological match can buffer predation by reducing predation risk (Pope et al., 1994), thus a phenological match could indirectly reduce top down pressure. Predation risk and competitive ability will also covary with smolt size. Finally, sockeye salmon smolts that compete with abundant odd-year pink salmon populations in the early marine environment have significantly lower growth and survival (Ruggerone et al., 2003). Future studies could include predator abundance or evaluate match/mismatches between salmon, their predators and competitors.

Given recent steelhead trout population declines in the northeast Pacific, it is timely to quantify patterns of ocean survival to begin to understand potential contributing factors. The Northwest Power and Conservation Council maintains a goal of a 4% average smolt-to-adult return rate (SAR) to facilitate viable Columbia River steelhead trout populations (NPCC, 2014), yet in eight of the twelve years observed, the Wind River population SAR has been lower than this threshold, with some years dropping below the lower end of the NPCC target range of 2 – 6%. Wind River steelhead trout have comparatively short migrations, passing only one dam, and therefore presumably experience less riverine and hydrosystem-induced mortality than upstream Columbia River populations. Considering its location in the hydrosystem, the fact that Wind River steelhead trout SAR is frequently below the

NPCC targets reveals that poor ocean survival, in addition to riverine and hydro-system survival, may compromise achieving NPCC viability goals. Because larger individuals have higher survival regardless of the degree of mismatch, it is possible that improvements in freshwater habitat quality that increase growth or size-at-age could buffer some wild steelhead and salmon populations from some of the effects of mismatch. However, since the majority of Wind River steelhead spend their final year rearing in canyon reaches with largely intact habitat (Buehrens and Cochran, 2018), it is not immediately clear what, if any, habitat improvements could be implemented to improve freshwater growth for our study population. Further, climate-driven decreases in habitat quality in both freshwater and ocean environments could have a compounding effect on steelhead trout ocean survival and population productivity.

Understanding the mechanisms contributing to variation in smolt-to-adult returns for Pacific salmon could facilitate better run-size forecasts. Steelhead trout are an important recreational fishery species, as well as important ceremonial, and subsistence fisheries for Tribes and First Nations. Yet, populations have declined dramatically in the last few decades. Incorporating a more detailed understanding of timing of food availability and energy requirements could help manage these important fish populations. We found that steelhead trout that enter an ocean environment with high quality prey at the base of the food web are more likely to survive than steelhead trout migrating in years when the biological spring transition date is late (after June 1st), and that larger fish are more likely to survive than smaller fish irrespective of degree of mismatch. Thus, phenological mismatches may impact marine fisheries population productivity, but it is important to consider the broader context in which these mismatches occur as other factors such as individual size can have an additive or ameliorative effect on the population-level response.

3.6 Acknowledgements

This project would not have been possible without the dedication and fortitude of WDFW, NOAA, and Oregon State University scientists and technicians that collected the two long term datasets used in this project: 1) the lifecycle monitoring of wild Wind River steelhead trout led by WDFW and 2) the biophysical monitoring including zooplankton biomass and community composition led by NOAA Northwest Fisheries Science Center and Oregon State University. We thank all the scientists and technicians involved in these projects; specifically, D. Rawding and C. Cochran of WDFW for designing and implementing Wind River life cycle monitoring; and William T. Peterson whose vision and scientific tenacity generated a continuous 20+ year ocean going sampling program along the Newport Hydrographic Line. Funding for S.M.W. was provided by Vanier Canadian Graduate Scholarship, Michael Stevenson Scholarship, and Steven Berkeley Marine Conservation Fellowship. Additional funding from the Liber Ero Foundation was for J.W.M. and the Banting Postdoctoral

Fellowship for K.L.W. We also thank D. Patterson, T. Williams, and members of the Salmon Watersheds Lab for feedback on the early manuscript.

3.7 Supplemental materials

3.7.1 Supplemental tables

Table 3.6: Annual Covariate Inclusion Model variable definitions and sources.

Variable	Time Frame	Model Term (δ_y)	Description	Reference
Biological Spring Transition Date	Annually	1	The first day cold-water northern and energy-dense zooplankton were found off the Oregon coast.	https://www.nwfsc.noaa.gov/
Spring Upwelling Transition Date	Annually	2	Date when the cumulative sum of Coastal Upwelling Index (beginning January 1) switched from decreasing to increasing.	www.cbr.washington.edu/dart/
Annual Upwelling Strength (mean)	March to June	3	Coastal Upwelling Index at 45°N 125°W.	www.cbr.washington.edu/dart/
Pacific Decadal Oscillation (PDO)	March to June	4	Composite North Pacific monthly sea surface temperature variability which trends over several decades.	http://research.jisao.washington.edu/pdo/
El Niño Southern Oscillation (ENSO)	April to June	5	Short term (6 – 18 month) anomaly of SST in the central and eastern tropical Pacific.	www.cpc.ncep.noaa.gov/
Southern Copepod Index	March to June	6	Anomalies in abundance of southern copepods (e.g., *Mesocalanus tenuicornis*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus pergens*, *C. arcuicornis*, and *C. parapergens*, *Calocalanus styliremis*, and *Corycaeus anglicus*).	https://www.nwfsc.noaa.gov/
Northern Copepod Index	March to June	7	Anomalies in abundance of northern copepods (e.g., *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*).	https://www.nwfsc.noaa.gov/
Sea Surface Temperature	March to June	8	Air temperature data from buoy stations; 46029 (46.14°N 124.49°W) and 46041 (47.35°N, 124.74°W).	www.ndbc.noaa.gov/
Aleutian Low Pressure Index (ALPI)	March to June	9	Anomaly of mean area (km^2) with sea level pressure <= 100.5 kPa in the North Pacific Ocean.	http://open.canada.ca/
Columbia River Discharge	April to June	10	Measured at the Bonneville Dam (USGS site 14128870; gauge height, ft).	https://waterdata.usgs.gov/
Ecosystem Indicator	Annually	11	Composite metric of 15 ecosystem indicators derived from principal component analysis.	https://www.fisheries.noaa.gov/

Table 3.7: Model average coefficients of the terms predicting ocean survival of steelhead smolts for the Biological Spring Transition Date Model.

Variable	Model Average Coefficient (95% CI)
FL	**0.495 (0.426, 0.568)**
RE	-0.122 (-0.317, 0.072)
$\boldsymbol{RE^2}$	**-0.126 (-0.195, -0.057)**
BIO	**-0.386 (-0.697, -0.067)**
BIO^2	0.091 (-0.167, 0.349)
Z	-0.031 (-0.200, 0.141)
$\boldsymbol{RE^*FL}$	**0.071 (0.005, 0.140)**
RE^* *Year*(2003)	-0.122 (-0.473, 0.206)
RE^* *Year*(2004)	-0.179 (-0.514, 0.125)
RE^* *Year*(2005)	-0.195 (-0.628, 0.207)
RE^* *Year*(2006)	0.324 (-0.011, 0.709)
RE^* *Year*(2007)	-0.087 (-0.349, 0.168)
RE^* *Year*(2008)	-0.148 (-0.133, 0.450)
RE^* *Year*(2009)	-0.005 (-0.277, 0.272)
$\boldsymbol{RE^*}$ ***Year*(2010)**	**0.357 (0.055, 0.699)**
RE^* *Year*(2011)	0.209 (-0.146, 0.609)
RE^* *Year*(2012)	0.025 (-0.312, 0.376)

(Continued on next page...)

Variable	Model Average Coefficient (95% CI)
$RE^*\ Year(2013)$	-0.193 (-0.497, 0.086)
$\boldsymbol{RE^*\ Year\ (2014)}$	**-0.290 (-0.604, -0.008)**
$FL^*\ Year(2003)$	0.040 (-0.152, 0.256)
$\boldsymbol{FL^*\ Year\ (2004)}$	**0.194 (0.016, 0.412)**
$FL^*\ Year(2005)$	0.170 (-0.075, 0.423)
$FL^*\ Year(2006)$	0.025 (-0.182, 0.231)
$FL^*\ Year(2007)$	-0.126 (-0.300, 0.037)
$FL^*\ Year(2008)$	-0.132 (-0.338, 0.072)
$FL^*\ Year(2009)$	-0.076 (-0.269, 0.116)
$FL^*\ Year(2010)$	-0.038 (-0.242, 0.150)
$FL^*\ Year(2011)$	0.010 (-0.233, 0.278)
$FL^*\ Year(2012)$	-0.042 (-0.284, 0.163)
$FL^*\ Year(2013)$	0.025 (-0.166, 0.214)
$FL^*\ Year(2014)$	-0.086 (-0.293, 0.104)

Variables include river exit date (RE), fork length (FL), total zooplankton biomass (Z), biological spring transition date (BIO). (*) indicates an interaction term. The $RE * Year$ interaction is the intra-annual mismatch term. Terms that have credible intervals that do not cross zero are bolded.

Table 3.8: Model average coefficients of annual terms predicting ocean survival of steelhead smolts.

Variable	Model Average Coefficient (95% CI)
Biological Spring Transition Date	**-0.324 (-0.601, -0.020)**
ALPI	-0.165 (-0.396, 0.120)
Spring Upwelling Transition Date	-0.416 (-0.131, 0.168)
Annual Upwelling Strength (mean)	0.223 (-0.106, 0.550)
Sea Surface Temperature	-0.430 (-0.162, 0.527)
ENSO	-0.169 (-0.514, 0.129)
PDO	**-0.391 (-0.660, -0.095)**
Columbia River Discharge	0.046 (-0.305, 0.387)
Southern Copepod Index	-0.286 (-0.622, 0.008)
Northern Copepod Index	0.136 (-0.130, 0.449)
Ecosystem Indicator	-0.390 (-0.671, -0.083)

Variables include Aleutian Low Pressure Index (ALPI), Pacific Decadal Oscillation (PDO), El Niño Southern Oscillation (ENSO). Bolded terms have 95% credible intervals that do not cross zero.

3.7.2 Supplemental figures

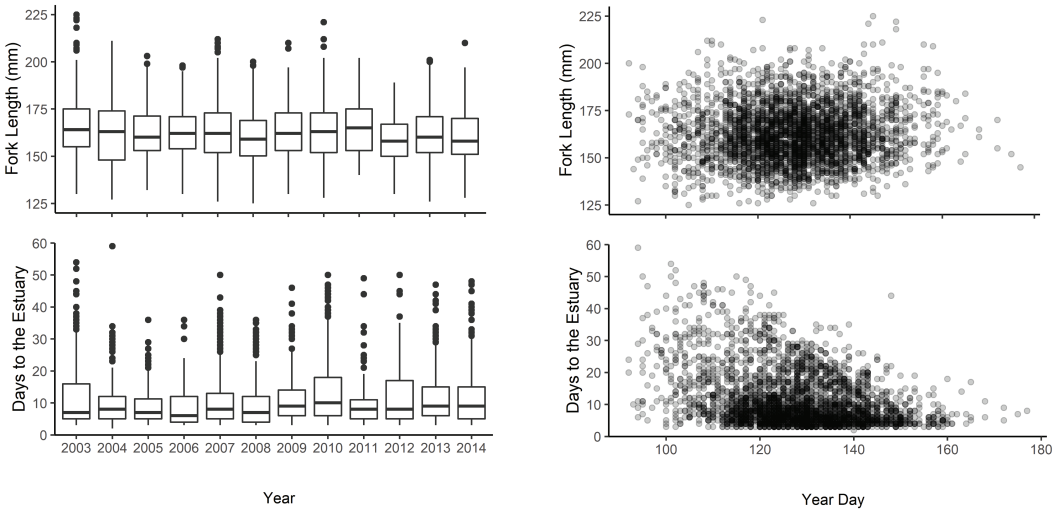

Figure 3.7: Inter-annual (left) and intra-annual (right) patterns in size (top) and outmigration duration (bottom) for outmigrating steelhead trout smolts from the Wind River. Migration duration calculated from a subset of the total number of tagged individuals that were subsequently detected at either Bonneville Dam or in the Columbia River estuary. This represents ~10% of the total number of tagged individuals.

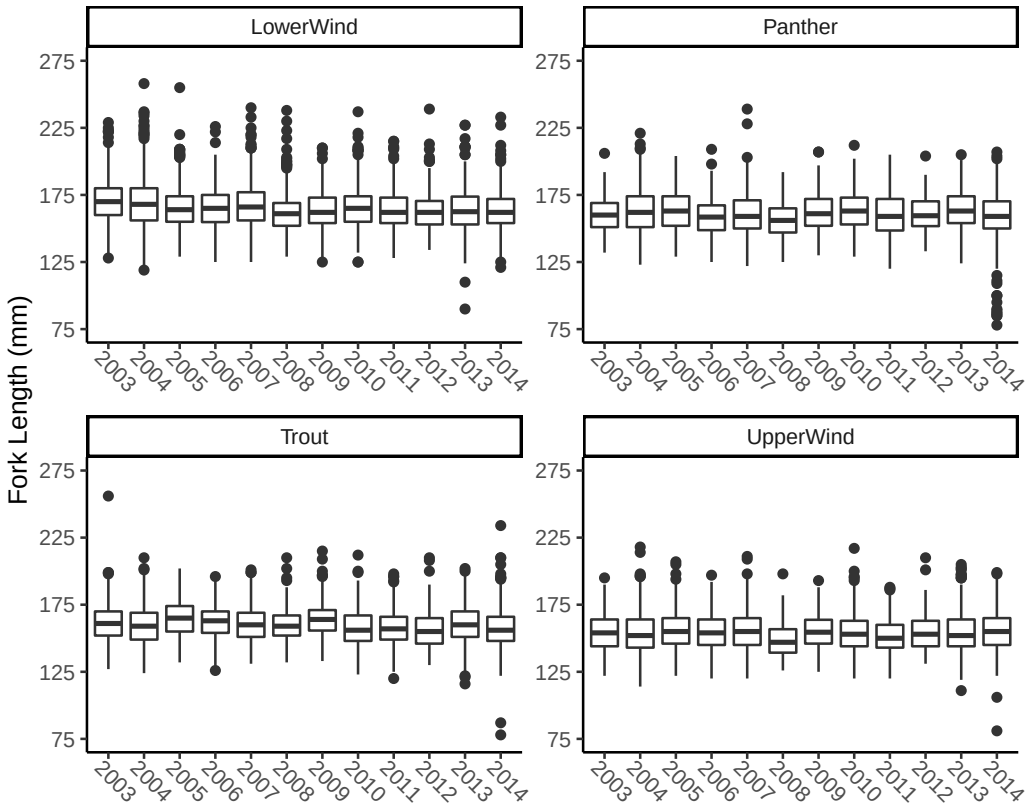

Figure 3.8: Size (fork length) of fish tagged at each of the Wind River capture locations across years.

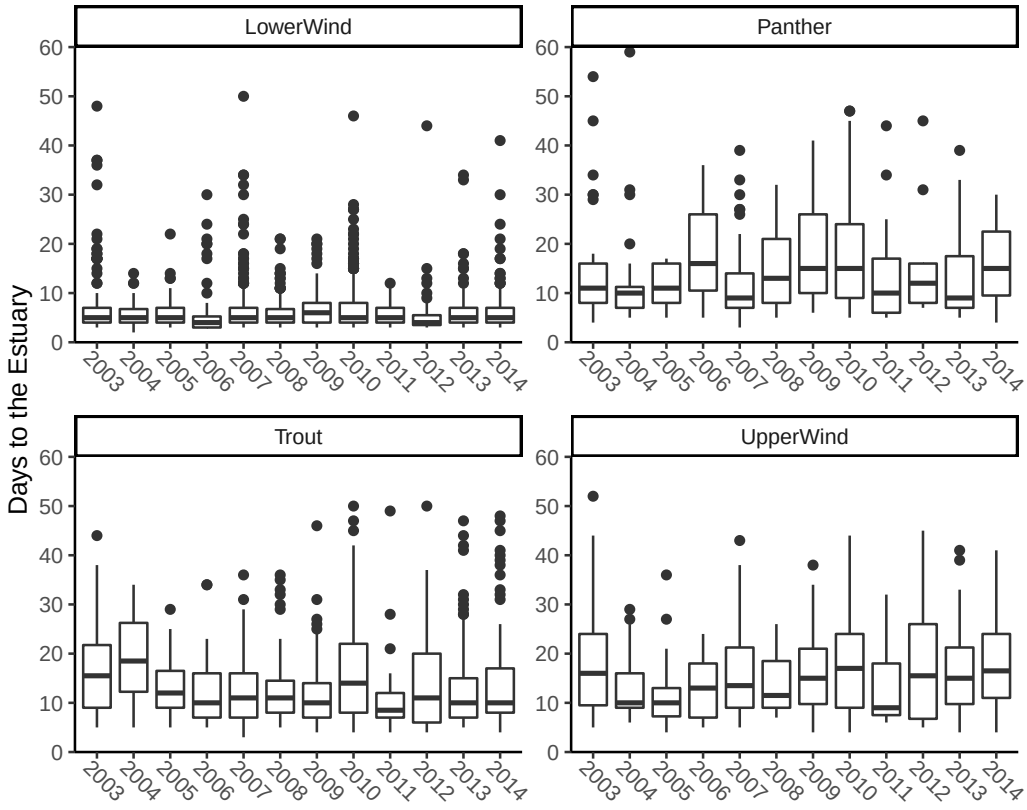

Figure 3.9: Migration rates for fish from tagging to estimated ocean entrance. Ocean entrance was measured as the date detected in the estuary in the mobile estuary PIT tag array or estimated by adding two days to the date that fish were detected at the Bonneville dam. Migration duration calculated from a subset of the total number of tagged individuals that were subsequently detected at either Bonneville Dam or in the Columbia River estuary. This represents ~10% of the total number of tagged individuals.

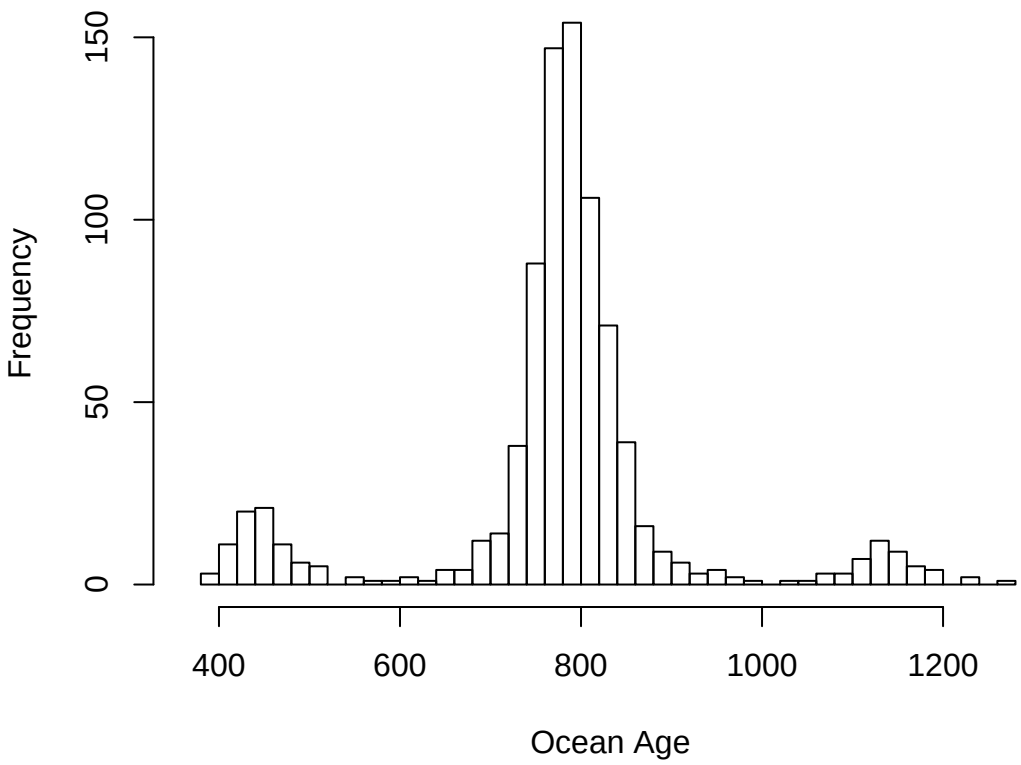

Figure 3.10: Days between tagging and maiden return of Wind River steelhead trout. Note the three peaks at ~1 year, ~2 years and ~3 years in the ocean. No fish spent more than 3 years in the ocean before completing their maiden spawning migration.

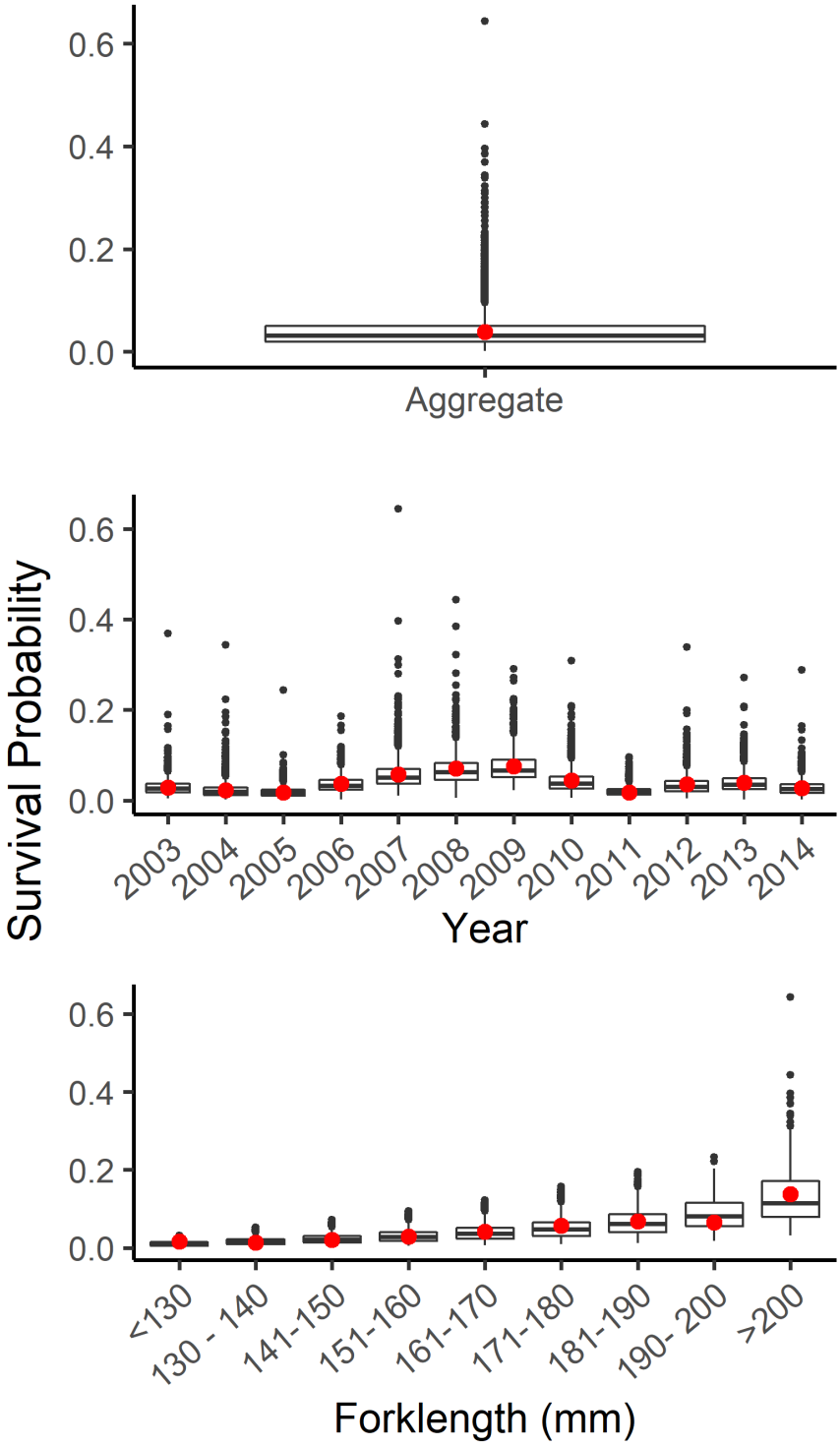

Figure 3.11: Posterior predictive checks comparing predicted survival (boxplots) with mean proportion surviving for all data (top), yearly survival probability (middle) and survival probability for size (bottom) for the Biological Spring Transition Date Model.

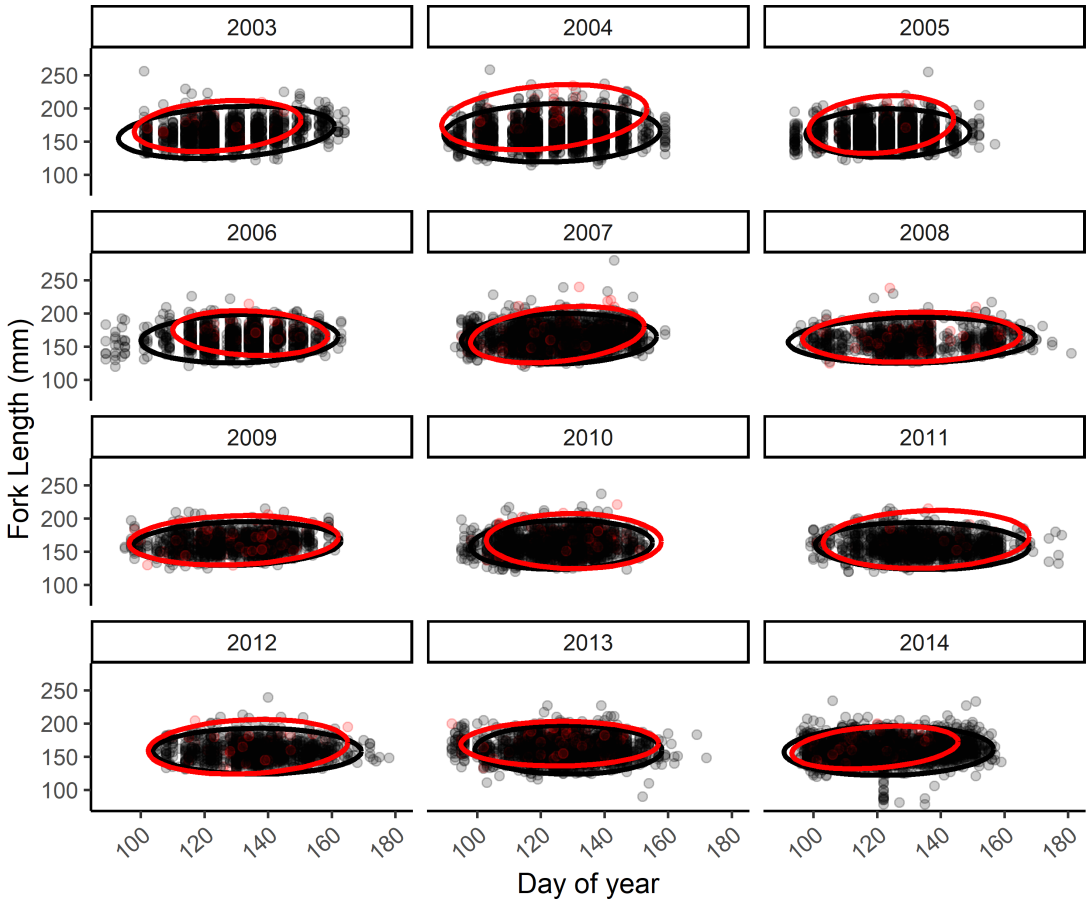

Figure 3.12: Fate of juvenile steelhead trout (red = survived, black = died) based on size (FL) and outmigration date. Ellipses represent 95% confidence area.

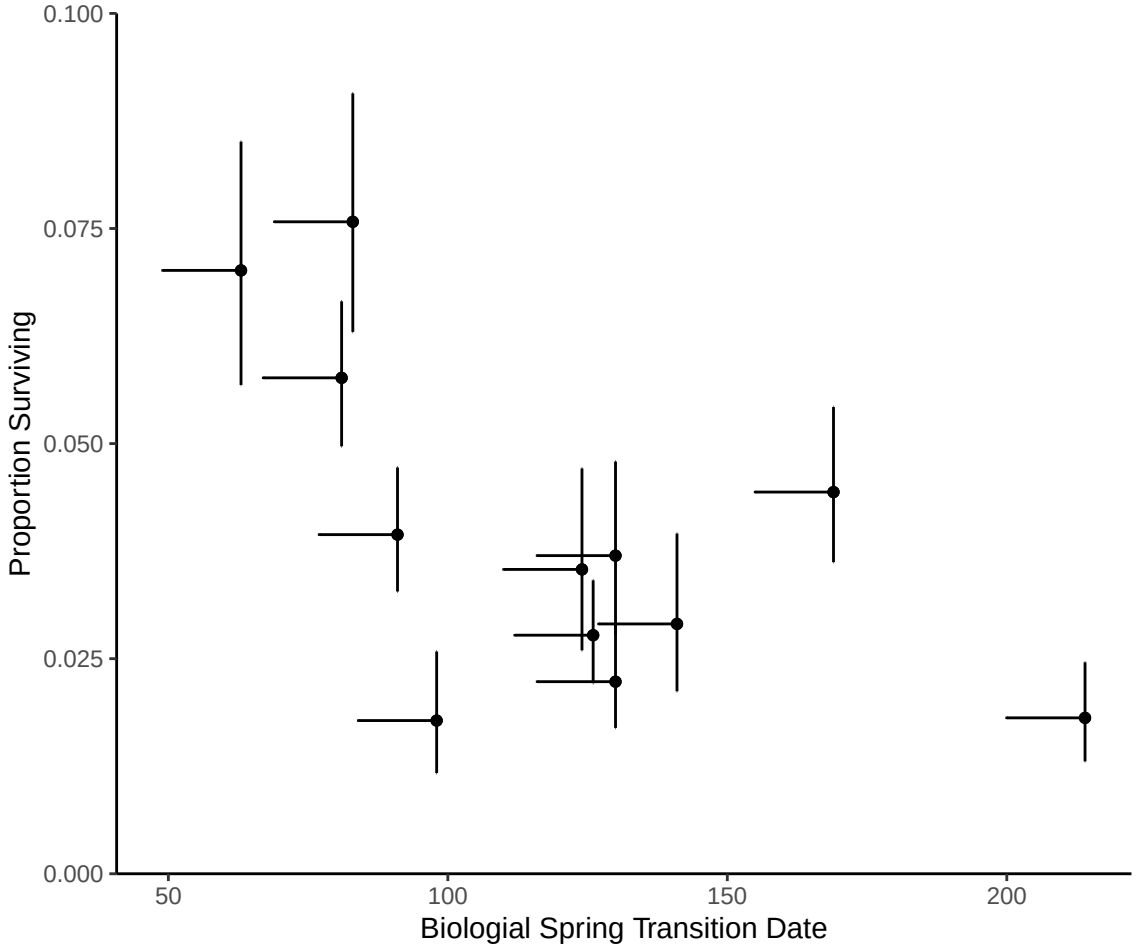

Figure 3.13: Relationship between biological spring transition date and the proportion of survivors during the same year. Vertical bars represent 95% credible interval. Horizontal error bars represent time between sampling events.

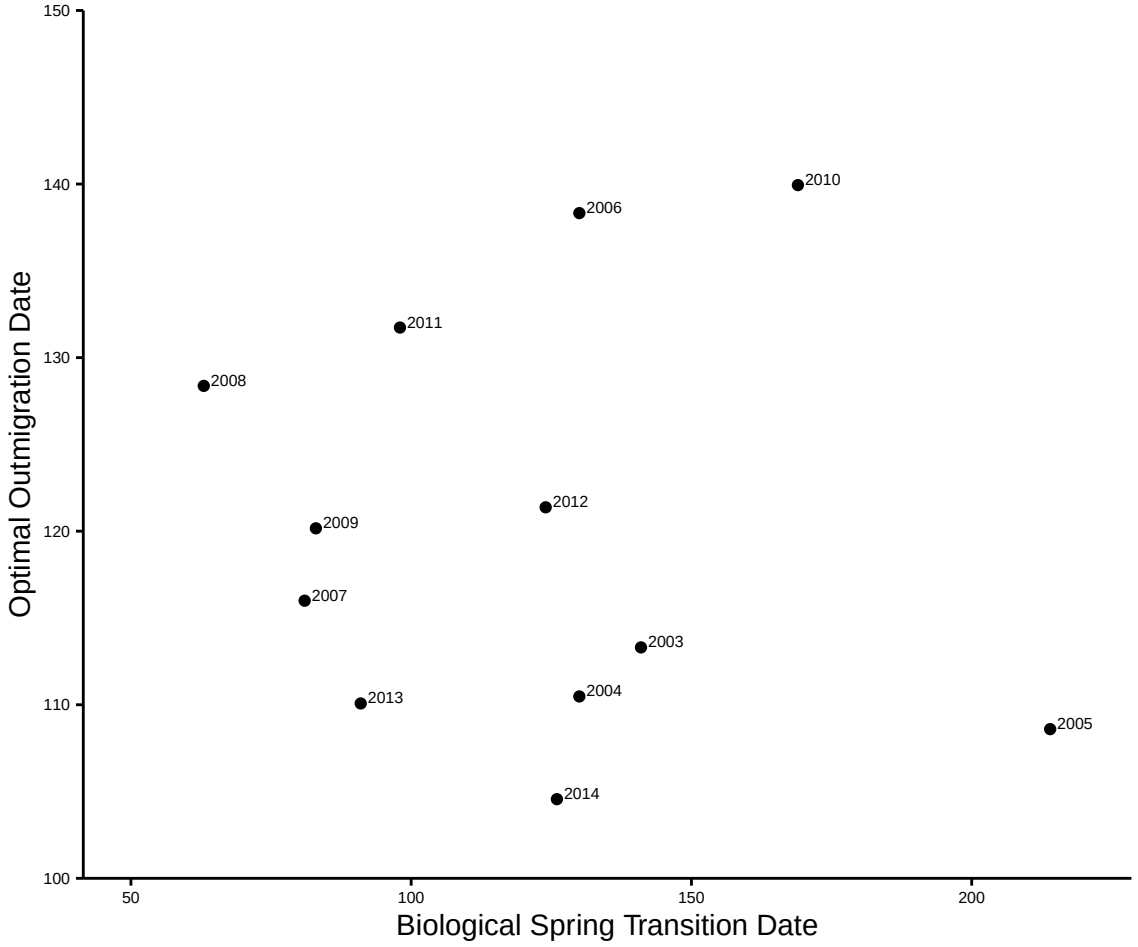

Figure 3.14: Relationship between biological spring transition date and the estimated optimal outmigration date for each year.

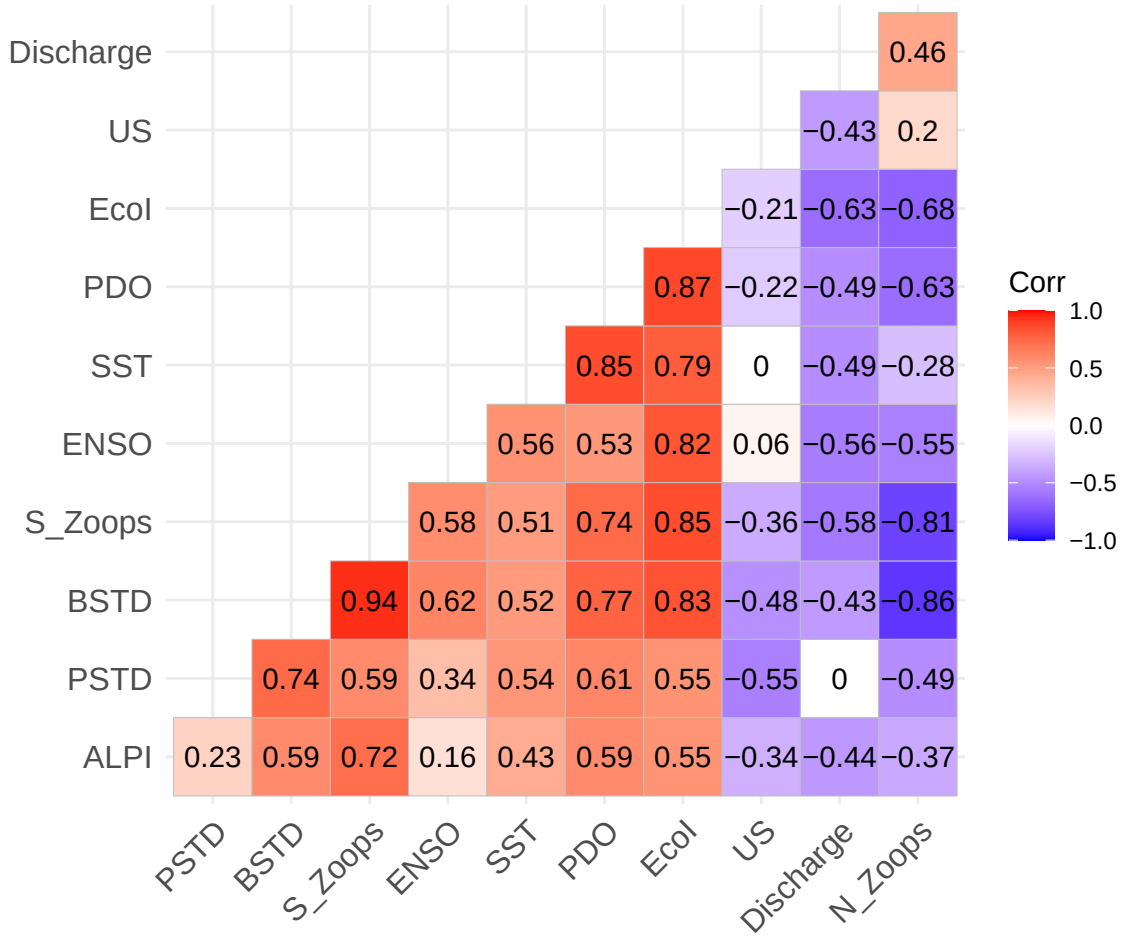

Figure 3.15: Correlation between annual covariates. Red indicates a positive correlation, while blue represents a negative correlation. The depth of the colour indicates the strength of the correlation, with darker colour having larger correlations. Annual covariates include mean April – June Columbia River discharge at Bonneville Dam (Discharge), mean March – June coastal upwelling strength at 45°N 125°W (US), NOAA salmon Ecosystem Indicator Index (EcoI), mean March – June Pacific Decadal Oscillation (PDO), mean March – June air temperature (SST), mean April – June El Niño Southern Oscillation estimates (ENSO), Southern copepod biomass anomaly (S_Zoops), biological spring transition date (BSTD), physical spring upwelling transition date (PSTD), Aleutian Low Pressure Index (ALPI), and Northern copepod biomass anomaly (N_Zoops).

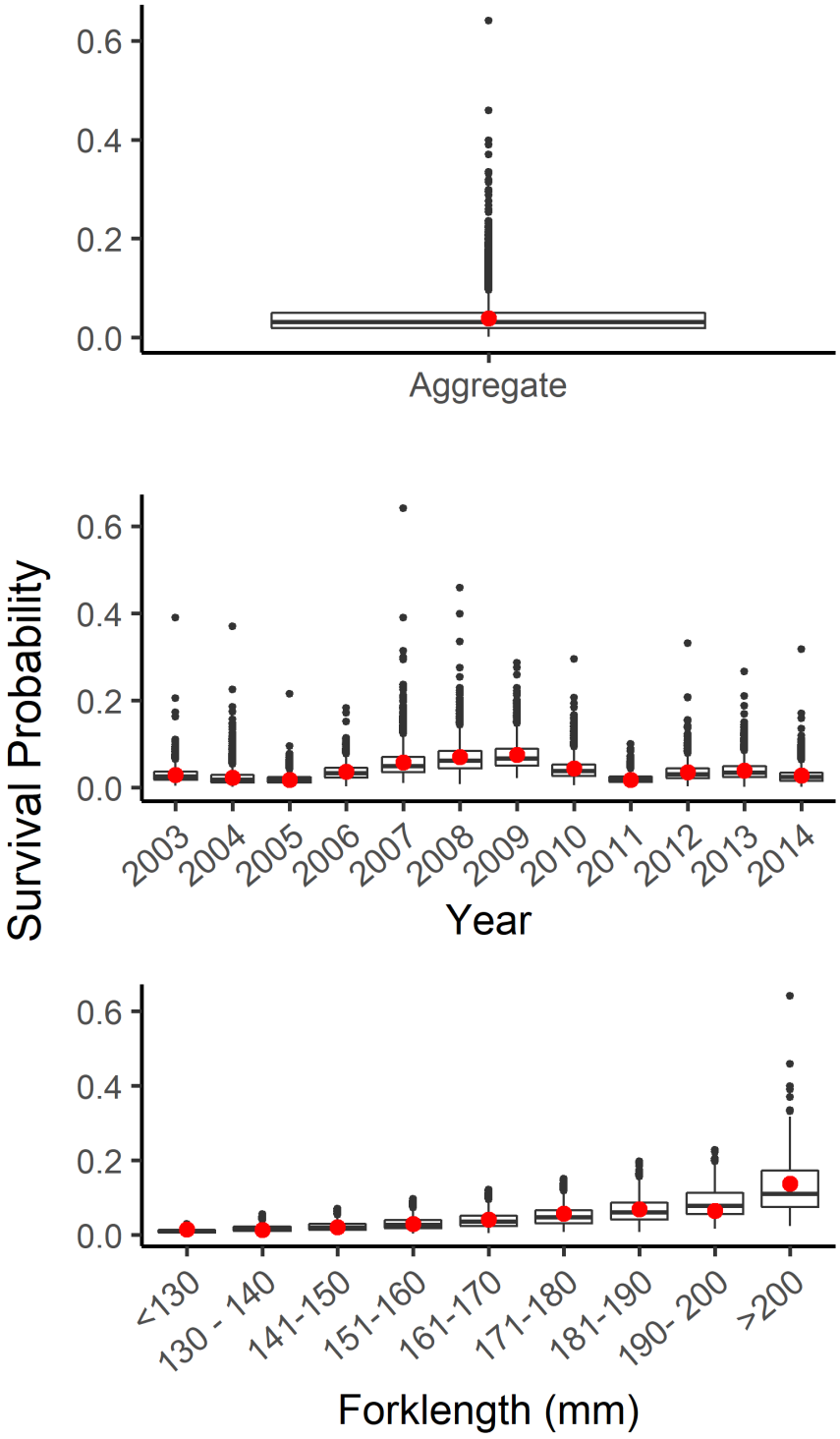

Figure 3.16: Posterior predictive checks comparing predicted survival (boxplots) with mean proportion surviving for all data (top), yearly survival probability (middle) and survival probability for size (bottom) for the Annual Covariate Inclusion Model.

3.7.3 Model code

Biological Spring Transition Date Model

JAGS model code for multi-level model. Note that model parameters are defined slightly differently in the manuscript to increase readability.

```
#Priors for inclusion parameters

pFLI ~ dbeta(1, 1) # uniform probability between 0 and 1
pREI ~ dbeta(1, 1) # uniform probability between 0 and 1
for (i in 1:n.year) {
iFLI.y[i] ~ dbern(pFLI) #inclusion probability for each FL by year interaction
iREI.y[i]~dbern(pREI) #inclusion probability for each RE by year interaction
}

w[6] ~ dbern(sum(iFLI.y) / n.year) # average of inclusion probability FL by year interaction
across all years
w[7] ~ dbern(sum(iREI.y) / n.year) # average of inclusion probability RE by year interaction
across all years

iFLM_tmp <- w[6] + ((1 - w[6]) * 0.5) # probability given inclusion/exclusion of w6, where w6
is interaction between FL and year
w[1] ~ dbern(iFLM_tmp)

iREM_tmp <- w[7] + ((1 - w[7]) * 0.5) # probability given inclusion/exclusion of w7, where w7
is interaction between RE and year
w[2] ~ dbern(iREM_tmp)

w[3]~dbern(.5)

iQM1_tmp <- w[2] * 0.5 #probability of w4(quadratic) given the base term is included (w2=1)
w[4] ~ dbern(iQM1_tmp)

w[8] ~ dbern(0.5)

iQM2_tmp <- w[8] * 0.5 #probability of w9(quadratic) given the base term is included (w8=1)
w[9] ~ dbern(iQM2_tmp)

iFLRE<-w[1]*w[2]*0.5 #if main effects are included, test for inclusion of interaction (FL X
RE)
w[5]~dbern(iFLRE)

#Individual/likelihood models
for (i in 1:n){
y[i] ~ dbern (p[i])
y.new ~ dbern (p[i]) # Monitor for posterior predictive tests
logit(p[i]) <- Xbeta[i]
Xbeta[i] <- int+w[1]*bet[1]*x1[i] +          # Size
                w[2]*bet[2]*x2[i] +          # River exit date- within year (base term)
                w[3]*bet[3]*x3[i] +          # Northern copepod biomass
                w[4]*bet[4]*pow(x2[i],2) +   # River exit date squared (quadratic term)
                w[5]*bet[5]*x1[i]*x2[i] +    # Interaction btwn size and river exit date (win
yr)
                w[6]*b.FL.y[year[i]]*x1[i] + # Interaction btwn size and year (across yrs)
                w[7]*b.TL.y[year[i]]*x2[i] + # Interaction btwn RE and year (across yrs)
                b.site.year[year[i],site[i]] # Nested effects of year (including group level
prior of biological transition date) and site
```

```
}

#Individual/likelihood model priors
for(i in 1:5){bet[i] ~ dnorm(0,1/1^2)}

#Group/prior models
## site is nested within year

for (j in 1:n.year) {
for (k in 1:n.site) {
b.site.year.std[j,k]<- b.site.year[j,k] - mean(b.site.year[,k])  #restandardizing betas for
within site, across years
b.site.year[j,k] ~dnorm(b.year.std[j],tau.site.year)}
b.year.std[j]<-b.year[j] - mean(b.year)
b.year[j] ~ dnorm (b.year.hat[j], tau.year)
b.year.hat[j] <-   w[8]*b.bio*bio_trans[j] +      # Biological transition date base term
                 w[9]*b2.bio*pow(bio_trans[j],2)  # quadratic term

}

for (j in 1:n.year) {
b.FL.y[j] <- FL.biotran[j] # the slope of the FL by year interaction term
FL.biotran[j] ~ dnorm(FL.biotran_slope*bio_trans[j], tau.fl.y)

}

for (j in 1:n.year) {
b.RE.y[j] <- RE.biotran[j]
RE.biotran[j]~dnorm(RE.biotran_slope*bio_trans[j], tau.tl.y) # slope of the time lag by year
interaction term

}


#Group/prior model priors

int ~ dnorm (0, 1/1^2)
b.bio ~ dnorm(0, 1/1^2)
b2.bio ~ dnorm(0, 1/1^2)
FL.biotran_slope ~ dnorm(0, 1/1^2)
RE.biotran_slope ~ dnorm(0, 1/1^2)

tau.year ~ dgamma(0.01,0.01)
tau.fl.y ~ dgamma(0.01,0.01)
tau.re.y ~ dgamma(0.01,0.01)

### site
tau.site.year ~ dgamma(0.01,0.01)
```

Annual Covariates Model

JAGS model code for multi-level model. Note that model parameters are defined slightly differently in the manuscript to increase readability.

```
#Individual/likelihood models

for (i in 1:n){
y[i] ~ dbern (p[i])
y.new[i] ~ dbern (p[i]) # Monitor for posterior predictive tests
logit(p[i]) <- Xbeta[i]
Xbeta[i] <- int+bet[1]*x1[i] +          # Size
                bet[2]*x2[i] +          # River Exit date - within year (base term)
                bet[3]*pow(x2[i],2) +   # River Exit date squared (quadratic term)
                b.TL.y[year[i]]*x2[i] + # Interaction btwn tl and year (across yrs)
                b.site.year[year[i],site[i]] # Nested effects of year (including group level
prior of biological transition date) and site
}

#Individual/likelihood model priors
for(i in 1:3){bet[i] ~ dnorm(0,1/1^2)}

#Group/prior models
## site is nested within year

for (j in 1:n.year) {
for (k in 1:n.site) {
b.site.year.std[j,k]<- b.site.year[j,k] - mean(b.site.year[,k])  #restandardizing betas for
within site, across years
b.site.year[j,k] ~dnorm(b.year.std[j],tau.site.year)}
b.year.std[j]<-b.year[j] - mean(b.year)
b.year[j] ~ dnorm (b.year.hat[j], tau.year)
b.year.hat[j] <- year_predict_choice[j]
}

for (j in 1:n.year) {
b.TL.y[j] <- TL.biotran[j]
TL.biotran[j]~dnorm(TL.biotran_slope*year_predict_choice[j], tau.tl.y) # this is the slope of
the time lag by year interaction term
}
```

```
#Variable Choice
index ~ dcat(pi[1:N]) # where N is 11 variables
pi[1:N] ~ ddirch(alphas[1:N])

for(i in 1:N){
alphas[i] <- 1/N
}

for (j in 1:n.year){
      year_predictor[j,1]<- b.bio*bio_trans[j]
      year_predictor[j,2]<- b.alpi*alpi[j]
      year_predictor[j,3]<- b.spr*spr_trans_date[j]
      year_predictor[j,4]<- b.upw*meanupw[j]
      year_predictor[j,5]<- b.tmp*meanTMP[j]
      year_predictor[j,6]<- b.oni*ONI_AMJ[j]
      year_predictor[j,7]<- b.pdo*PDO_MAMJ[j]
      year_predictor[j,8]<- b.flow*amjflow[j]
      year_predictor[j,9]<- b.s*amjanomS[j]
      year_predictor[j,10]<- b.n*amjanomN[j]
      year_predictor[j,11]<- b.eco*Ecosystem.Indicators[j]
      year_predict_choice[j]<- year_predictor[j,index]
}

#Group model priors

int ~ dnorm (0, 1/1^2)
TL.biotran_slope ~ dnorm(0, 1/1^2)
tau.year ~ dgamma(0.01,0.01)
tau.tl.y ~ dgamma(0.01,0.01)

### site
tau.site.year ~ dgamma(0.01,0.01)


#choice priors
b.bio ~ dnorm(0, 1/1^2)
b.alpi ~ dnorm(0, 1/1^2)
b.spr ~ dnorm(0, 1/1^2)
```

```
b.upw ~ dnorm(0, 1/1^2)
b.tmp ~ dnorm(0, 1/1^2)
b.oni ~ dnorm(0, 1/1^2)
b.pdo ~ dnorm(0, 1/1^2)
b.flow ~ dnorm(0, 1/1^2)
b.s ~ dnorm(0, 1/1^2)
b.n ~ dnorm(0, 1/1^2)
b.eco ~ dnorm(0, 1/1^2)
```

Chapter 4

Limits on performance and survival of juvenile sockeye salmon during food deprivation: a laboratory-based study

4.1 Abstract

Long distance migrations can be both energetically demanding and represent phases of high mortality. Understanding relationships between body condition and migratory performance can help illuminate the challenges and vulnerabilities of migratory species. Juvenile anadromous sockeye salmon (*Oncorhynchus nerka*) may migrate over 1000 km from their freshwater nursery habitats to estuary and ocean feeding grounds. During the period corresponding to the seaward migration of sockeye salmon, we held smolts in the laboratory to ask: 1) Does non-feeding migration duration influence prolonged swim performance and survival? and 2) what are the relationships between individual body condition and swim performance and survival? Wild sockeye salmon were intercepted during their migration and held without food for up to 61 days to represent the non-feeding freshwater migration and the extremes of poor estuary habitat. We conducted 40 sets of prolonged swim trials on 319 fish from three treatment groups which represented entrance to the marine environment on a 1) average, 2) delayed, and 3) severely delayed migration schedule. Experimentally controlled freshwater migration duration did not impact swim performance or survival. Swim performance decreased concomitant with condition factor, where smolts with a Fulton's

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condition factor of <0.69 were less likely (<50% probability) to complete the swim test (90 min swim test, at ~0.50 m/s). Survival of salmon smolts in the lab was less likely at energy densities of less than 3.47 MJ/kg. Swim performance decreased much sooner than survival, suggesting that swim performance and therefore condition factor, may be a good indicator of survival of migratory smolts, as fish with reduced swim performance will likely be predated. These two relationships, one more ecologically relevant and one more clinical, help reveal the limits of long-distance migration for juvenile salmon and can be used to determine population-specific starvation risk associated with various freshwater and marine habitat conditions.

4.2 Introduction

Long distance migrations are often challenging life-history phases with higher mortality rates compared to stationary phases (Sillett and Holmes, 2002; Alerstam et al., 2003; Klaassen et al., 2014; Clark et al., 2016; Lok et al., 2015). Migratory success or failure may be controlled by variation in individual condition and energetics within and across populations. For instance, body condition can be a strong indicator of migration success (Drent et al., 2003; Duijns et al., 2017), as long distance migrants often rely heavily on endogenous energy stores to fuel migrations (McKeown, 1984; Dingle, 1996), and could be a potential tool for predicting migration success. For example, red knots (*Calidris canutus rufa*) with higher body condition (size-corrected mass) had faster migration to breeding grounds, higher migration success (survival), and were more likely to have bred successfully, than those of lower body condition (Duijns et al., 2017). Lower quality individuals are also more likely to be predated during migration (Dierschke, 2003; Tucker et al., 2016). Thus, body condition at the beginning of the migration can influence subsequent performance, thereby driving carryover effects across life-stages and habitats. Understanding the relationship between body condition and the survival of migrating animals could help clarify their limits and vulnerabilities to environmental or anthropogenic disturbances in habitat or migratory conditions.

While energy and migration success are presumably related for many populations (Drent et al., 2003), these relationships remain relatively poorly described for many important migratory species. It is possible that there is an abrupt threshold, where performance remains robust until physical or energetic condition decreases to a threshold at which point performance decreases dramatically. Alternatively, the relationship could be more linear, where a unit decrease in condition would result in a proportional decrease in performance (Huggett, 2005; Ficetola and Denoël, 2009). It is also possible that there is not a single condition metric that accurately predicts performance given the number of different physiological processes that support a single type of performance. Understanding the form of condition-performance relationships, and the thresholds they may contain, is important for predictions

of migration success. For example, identifying an energetic condition-performance threshold could help identify the proportion of individuals in a population that may be at risk of not completing their migration. Such thresholds could also be used to understand the vulnerabilities of different populations to changes in migratory conditions, such as anthropogenic flow alteration that results in slowed migration rates (Raymond, 1968, 1979).

Juvenile Pacific salmon (*Oncorhynchus* spp.) complete long distance, and sometimes energetically-expensive, migrations from their natal rearing lakes and streams to estuarine and ocean feeding grounds (Brett, 1995; Hinch et al., 2006). These freshwater migrations range in distance from tens to over a thousand kilometers and can take anywhere between a few days to several weeks to complete (Johnson and Groot, 1963; Groot and Margolis, 1991; Quinn, 2005; Clark et al., 2016). Many authors suggest that during this time smolts do not feed extensively and instead primarily use endogenous energy stores (Stefansson et al., 2003; Quinn, 2005; Hinch et al., 2006), although it should be noted that direct empirical evidence is scant, and the evidence that has been recorded is mixed (Larsson et al., 2011). Indeed, endogenous energy stores of long-distance migrating smolts can approach very low levels (Stefansson et al., 2003; Rondorf et al., 1985). For example, Rondorf et al. (1985) found that whole body lipids of hatchery-origin Chinook salmon (*O. tshawytscha*) migrating in the Columbia River decreased from 4.3% to 1.4% (a 65% decline) during the ~700 km migration between the release site and the estuary and that survival was higher for fish that had higher percent body lipid at the time of their release (Rondorf et al., 1985). Thus, endogenous energy levels may decrease to very low levels during freshwater migration.

The physiology and energetic condition of individual fish could control their performance during migration. Under typical migration conditions, migrating fish rely primarily on fats and proteins for fuel (Driedzic and Hochachka, 1978; Brett and Groves, 1979). Fish migrants also commonly use protein during periods of food deprivation. However, during periods of starvation, protein catabolism can compromise muscle tissue and likely comes at the expense of performance (Moon and Johnston, 1980; Sullivan and Somero, 1983; Black and Love, 1986; Kiessling et al., 1990; Martinez, 2003). Thus, prolonged swim performance should decline as protein content declines. Lipid levels of 1.4 – 2.0% are thought to be the lowest levels possible, as the remaining lipids are likely structural phospholipids of cell walls and are essential for survival (Castledine and Buckley, 1980). Indeed, Pacific salmon smolts are rarely observed to have lipid levels lower than 2.0% in the wild (DFO unpublished data), suggesting that this may be a threshold for survival. Therefore, migration success seems likely to be positively related to body condition, especially lipid levels. Furthermore, both condition and ionoregulation could shift through time during migration (Berggren and Filardo, 1993; Bassett et al., 2018) and affect swim performance and survival during initial transfer to saltwater. Thus, the duration of freshwater migration could also influence swim performance and survival upon transition to saltwater.

It has proven challenging to link observed changes in physical or energetic condition during migration to performance or survival. Few studies have examined swim performance of salmon smolts in relation to condition (Bams, 1967; Snyder, 1980). More have studied condition-dependent survival, but mostly with hatchery fish in a lab setting (LeBrasseur, 1969; Connolly and Petersen, 2003; Simpkins et al., 2004, 2003; Ferguson et al., 2010) with several attempting to infer condition and survival from natural settings (size: Ricker 1954; Ward et al. 1989; Henderson and Cass 1991; proximate body condition: Gardiner and Geddes 1980; Biro et al. 2004; Finstad et al. 2004). Thus, there is a need for robust laboratory studies of the relationship between condition, performance, and survival of outmigrating wild salmon.

Here we quantified the relationship between freshwater migration duration, body condition, swim performance, and survival in a wild population of migratory sockeye salmon (*O. nerka*) held in a laboratory environment. Specifically, we asked – 1) How does duration of freshwater migration impact swim performance and survival? What are the relationships between energetic and physical condition and 2) prolonged swim performance or 3) survival? We found that freshwater migration duration did not influence prolonged swim performance or survival. We compared energetic condition metrics (i.e., proximate body composition and derived energy values) and physical condition (i.e., size, weight, and condition factor) and found that condition factor best predicted prolonged swim performance, whereas energy density and protein content were predictive of survival. The swim performance threshold occurred approximately five weeks before the survival threshold, suggesting that swim performance may be a more biologically relevant endpoint for predicting survival in wild juvenile salmon. As a result, condition factor could be a useful tool for understanding how changes to freshwater habitat, which impact fish condition, could affect survival during seaward migration and the early marine life stage of salmon.

4.3 Methods

4.3.1 Overall study approach

We held juvenile sockeye salmon smolts without food for 61 days in three treatment groups modelled after freshwater migration durations of the Chilko Lake sockeye salmon population used in this study: 1) transferred to saltwater after 7 days, 7D group – which matches closely with the average migration duration of Chilko Lake salmon smolts, 2) transferred to saltwater after 14 days, 14D group – representing a delayed migration, and 3) transferred to saltwater after 21 days, 21D group – representing a severely delayed migration (Fig. 4.1). Different smolts from each of the three treatment groups completed a prolonged swim performance challenge each week for six weeks, until for two successive weeks, >80% of fish could not finish the trial (swim performance endpoint). After the swim trials were completed, we continued to observe fish for mortality, and once half of the remaining fish

being held had died (n = 78, survival endpoint) the experiment was terminated. After 28 days of food deprivation, we began feeding a subset of the 7D treatment group to monitor swim performance during recovery from starvation (n = 36). Approximately nine different fish from this fed group completed swim performance trials each week for five weeks to determine whether swim performance could be recovered after a period of food deprivation. The re-feeding experiment would ensure that energetic condition was the main factor that changed during holding and that a decrease in condition was related to a decrease in swim performance, rather than an artifact of holding time. We compared swim performance and survival between the three migration duration treatment groups and found no difference between groups. Since there was no difference between groups, we measured and calculated a variety of energy condition metrics (i.e., energy density, lipid content, moisture content, protein content, and triglyceride (TAG) concentration) for the 7D group (a subset of fish swam in experiment 1), and all the fish that died to determine the relationship between condition and prolonged swim performance (experiment 2) and survival (experiment 3).

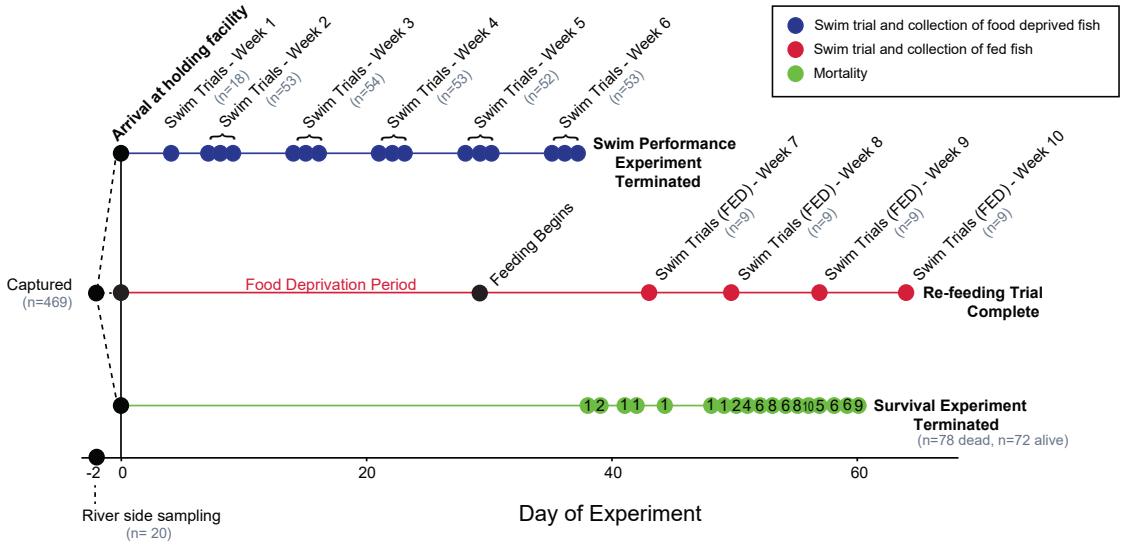

Figure 4.1: Experiment timeline, where fish were captured and a subset were sampled at the river (Day -2), before transportation to a holding site on Day 0. Fish were distributed evenly among three treatment groups (7D, 14D, 21D) and among three tanks within each group, for a total of nine tanks. Fish either were food deprived and completed a swim performance trial each week for six weeks (blue), held for 28 days before feeding for two weeks and then completed swim performance trial weekly for four weeks (pink), or held without food until death (green). Fish were randomly selected for swim trials across tanks from each treatment group for the swim performance experiment. A randomly selected subset from the 7D group, were moved to a different tank and fed for the re-feeding trial. Grey 'n' indicates the number of different fish that completed the swim trial each week. Black 'n' indicates the daily mortality in the survival experiment.

4.3.2 Fish collection

Wild juvenile sockeye salmon were caught during their seaward migration at the outlet of Chilko Lake (51.63N, -124.14W). Chilko Lake is an indicator population for management of Fraser River sockeye salmon and is one of the most productive sockeye salmon lakes in the Fraser River basin, producing an average of ~30 million sockeye salmon smolts annually (1994 – present running average). The predominate age class of Chilko Lake smolts is age 1, however Chilko Lake produces some 2-year-old smolts typically ranging from ~2 – 10% of the total outmigration cohort. Only 1-year-old fish (i.e., fish with fork lengths of less than 110 mm) were used in this study. Migration takes ~4 – 12 days as smolts travel the ~700 km from Chilko Lake through the Chilko, Chilcotin, and Fraser Rivers to the Strait of Georgia (Clark et al., 2016; Stevenson et al., 2019). It takes an additional 30 – 45 days before salmon leave inland coastal waters after traversing the Strait of Georgia and Johnstone Strait (Clark et al., 2016; Stevenson et al., 2019). Previous work has shown that Chilko sockeye salmon smolts migrate at a rate of ~30 – 220 km/day in freshwater and ~10 – 25 km/day in the marine environment along the east coast of Vancouver Island (Welch et al., 2009; Clark et al., 2016; Stevenson et al., 2019).

Juvenile sockeye salmon were captured by dip net on the evening of May 3, 2017 at the Chilko smolt enumeration fence, a full fence weir managed by Fisheries and Oceans Canada Fraser River Sockeye Stock Assessment Program. Twenty fish were euthanized on site with an overdose of MS222 (0.5 g/L) and preserved at -80°C for energetic analysis. Remaining fish were held overnight in an aerated 1000 L holding tank (5.8 – 7.5°C; 80.1 – 109.9% O_2 saturation) and the next day were driven ~12 h to the holding facility at Simon Fraser University in Burnaby, BC. The present study was conducted in accordance with the Canadian Council on Animal Care, as administered by Simon Fraser University (1238B-17).

4.3.3 Fish holding

Smolts were divided into the three treatment groups, 7D (n = 179), 14D (n = 180), and 21D (n = 182) and were randomly assigned to three tanks per treatment, thus sockeye salmon smolts were held in nine oval holding tanks (200 L) for up to 64 days (61 days for survival experiment, and 64 days for fed treatment; May 4 – July 7, 2017; Fig. 4.1) at a density of <2 smolts per litre. Water was flushed through the tanks at a rate of >2 L per minute. Holding tanks were covered with plexiglass, half of which was black to allow for shading in the tanks. A single air stone was used to enhance oxygen saturation, which never decreased below 90% in any tank (Handy Polaris, OxyGuard Internation A/S, Farum, Denmark). Smolts were originally held in dechlorinated and UV sterilized freshwater and were transitioned to saltwater at the three respective time points (7D, 14D, 21D). Fish in each group were transitioned gradually over 36 hrs to saltwater at a similar concentration to what they would experience during migration through the Fraser River estuary and coastal

Vancouver Island (~28 – 30 ppt; Thomson 1981). Saltwater was made to a concentration of ~28 – 30 ppt (Instant Ocean® Sea Salt) and allowed to sit for 24 hrs before being added to the circulation system. As it was being recirculated among tanks, saltwater was filtered through carbon filters. Approximately 30% of saltwater was replaced every two to three days to keep ammonia concentrations below 2 ppm. Water temperature was held constant with a mean of 10.7°C (7.8 – 12.9°C) consistent with ambient May/June Fraser River water temperature (MacDonald et al., 2019). A water pump temporarily went out on June 6, 2017 and water temperature increased in all tanks to 13 – 14.5°C for ~14 hrs, no mortalities were recorded resulting from that event and 14.5°C is within the range of temperatures experienced by smolts in the natural environment. Smolts were held in 12:12 hr light:dark conditions.

Holding tanks were checked at least twice daily. Dead fish were removed, fork length (mm) and weight (g) were recorded and fish were frozen at -80°C for later analysis. Any distressed fish, characterised by gasping at the water surface or loss of equilibrium, were euthanized with an overdose of MS222 (0.5 g/L). Food was withheld from fish in the nine tanks until approximately half of the fish had died. Remaining fish were euthanized with an overdose of MS222 (0.5 g/L). All fish were measured, weighed, and frozen at -80°C for later analysis.

4.3.4 Re-feeding

After 28 days of food deprivation, we transferred a subset of 36 smolts from the 7D group to a 150 L holding tank and began feeding them (7D-fed) twice daily with commercial pellets (EWOS Canada Ltd. Surrey, Canada) in excess (~2% body weight). Nine different fed fish were swum each week after 2, 3, 4, and 5 weeks of feeding.

4.3.5 Swim flume

Prolonged swim performance tests were completed in a fixed velocity flow-through swim flume (14 cm wide, 25 cm tall, 240 cm long; a plexiglass insert was used to narrow the swim arena to 9 cm wide, 15 cm tall, 142 cm long to increase water velocity), where water was pumped into the front of the flume, flowed through a honeycomb structure to increase laminar flow, and through a mesh net out the back into a recirculating tank. At the farthest end of the flume, a vertically sliding plexiglass door could be adjusted to ensure the water level in the flume was at 15 cm. A black plastic cover provided shade in the center of the flume and lights in front and behind the shaded region were used to encourage fish to swim in the shaded middle of the swimming arena where the flow was most consistent. Flow was measured at the top, middle, and bottom of the water column in both salt and freshwater.

4.3.6 Prolonged swimming experiment

Of the three types of swim performance tests (burst swim performance (<2 min), prolonged swim performance (<120 min) or critical swim speed tests (>120 min); Beamish 1978), we chose to perform prolonged swimming trials as they are rooted in biological realism and are related to fish condition and health (Beamish, 1978). Prolonged swim performance affects migratory capacity, as well as the ability of fish to capture prey, and evade predators, and thus is linked to survival and fitness (Plaut, 2001).

Smolts from each of the three groups underwent a swim performance trial each week for six weeks to determine if swim performance differed between treatments groups (experiment 1) as well as across differing physical or energetic condition (experiment 2). Six swim trials were performed every week (two trials for each of the three treatment groups), with nine fish in each trial (18 from each of the three treatment groups), for a total of ~54 fish swum each week. The swim trials in the first week were an exception in which, due to time constraints, we swam six fish from each group randomized over two trials, and across all holding tanks. These fish were unmarked and were not assigned to a treatment group, therefore they provide a baseline swim performance for all groups, but were excluded from swim trial analysis. Fish were always swum in water of the same condition (i.e., salinity, temperature, oxygen saturation) as they were being held. Fish from each treatment group were randomly assigned to each swim trial, when possible given different holding salinities. For example, during the second week only the 7D group fish were in saltwater so they were swum in two trials (nine 7D fish in each trial), whereas both the 14D and 21D groups were in freshwater and were therefore randomly assigned to four trials (four to five fish from the 14D and 21D groups in each trial). Two trials were completed each day, with the order of trials randomised each week. Each trial consisted of two swim performance tests, one in the morning and one repeat test in the afternoon on the same fish to assess repeatability of performance. Repeat swim performance data are available in the supplemental information (Fig. 4.7). The evening before each swim trial, 18 fish were removed from their holding tanks and individually marked using a fin clip. Fish were anaesthetised in MS222 (0.05 g/L), and the tips of the ventral and/or anal fins were clipped, enabling unique identification of each fish. Fish were recovered overnight in two 150 L aquarium with nine fish in each tank. For fish that were being fed, food was withheld 24 hrs before the swim trial was completed. We chose to cease swim trials after six weeks as >80% of the different fish swum in each trial could not finish the first test in two consecutive weeks (weeks 5, 6; swim performance endpoint).

For each test, nine individually marked fish were placed in the swim flume for a 12 min acclimation period at a flow rate of ~0.085 m/s (~1 BL/s). Following the acclimation period, flow rate was steadily increased to 0.50 m/s (~4.5 – 6.4 BL/s) over a period of 12 min. Fish that did not swim before the flume reached full flow were gently prodded three successive

times with a blunt instrument to encourage swimming. If they still refused to swim, they were removed from the study. Once at 0.50 m/s, flow rate was held constant for 90 min (pilot swim tests in week 1 confirmed 90 min was required to achieve variability in swim performance). Fish that fell to the mesh net at the back of the flume were gently prodded three successive times with a blunt instrument to encourage swimming. If they remained at the back mesh, the time was recorded to the nearest 10 sec and the fish was removed from the flume and placed in a glass aquarium for the remainder of the trial. Fish were allowed to rest for at least two hours before the swim test was repeated. After completing the second swim test, fish were euthanized with an overdose of MS222 (0.5 g/L). Fish were weighed (g), fork length (FL; mm) was measured and fish were frozen on dry ice and stored at -80°C until analyses.

4.3.7 Body condition analyses

Of the fish that participated in the swim performance trials, we only measured the energetic condition of fish from the 7D (n = 179) and 7D-fed (n = 36) groups, because all three unfed treatments (7D, 14D, and 21D) had similar swim performance and the 7D group was most biologically consistent with natural migration duration/timing of Chilko Lake sockeye smolts. Physical condition was assessed for all treatment groups by measuring fork length (mm) and wet mass (g) and by calculating Fulton's condition factor (Equation 4.1). We determined proximate body composition (moisture, lipid, and protein content) for all fish that died during, or were alive at the end of the experiment, as well as the fish from the 7D and 7D-fed groups that underwent the swim performance trials. Carbohydrate content was not determined as food was withheld prior to collection, and carbohydrates such as muscle and liver glycogen are not a significant source of stored energy in fish (Brett, 1995), rather lipid and protein are the main fuel used by fish during periods of food deprivation (Driedzic and Hochachka, 1978; Brett and Groves, 1979; McKeown, 1984). We decided to measure triglycerides (TAG), in addition to all lipid content, as TAG is the main form of stored lipids in vertebrates (Driedzic and Hochachka, 1978) and therefore their depletion could represent a decrease in energy condition (Cleary et al., 2012).

Proximate body analysis was completed according to methods of Crossin et al. (2003) that were adapted from Higgs et al. (1979) and Bligh and Dyer (1959). Briefly, whole fish were homogenized in a SPEX SamplePrep 2010 Geno/Grinder (SPEX, Metuchen, NJ) at 1500 rpm for two-minute intervals until completely homogenized. A sample of 0.3 g ± 0.015 g of homogenate was weighed for each of lipid, water, and ash analysis. Together, lipid, water, and ash percentages can be used to calculate protein content and energy density.

4.3.7.1 Lipid extraction

A mixture of methanol, chloroform, and water in ratio of 1:1:0.48 was added to the sample and homogenized. Samples were filtered with a Büchner funnel and the supernatant was

decanted into a graduated cylinder. Once biphasic layers of chloroform-lipid and methanol-water formed, the volume of the lipid-chloroform layer was measured, and the top water-methanol solution was aspirated away. A 100 μl sub-sample of the lipid-chloroform layer was removed and stored at -80°C for determination of TAG concentration. The remaining chloroform-lipid solution was pipetted into pre-weighed aluminum boats and the remaining lipid was weighed when chloroform had completely evaporated. All samples were analyzed in duplicate, and only samples that differed by less than 0.5% were retained. Lipid values are reported in percent lipid of total fish wet mass.

4.3.7.2 Percent water

Whole body moisture content was determined by drying a 0.3 g ± 0.015 g sample of homogenate in an oven overnight (16 – 20 h) at 100°C. Samples were then placed in a desiccator for 15 min and weighed. All samples were analyzed in duplicate, and only replicates that differed by less than 1.5% were retained. Body moisture values are reported in percent water of total fish wet mass.

4.3.7.3 Ash

A 0.3 g ± 0.015 g sample of each homogenate was transferred to the furnace and combusted at 600°C for 2.5 hrs. Samples were placed in a desiccator for 15 min and then weighed a final time. All samples were analyzed in duplicate, and only samples that differed by less than 0.5% were retained.

4.3.7.4 Triglycerides

TAG concentration was determined using a colorimetric assay kit (Cayman Chemicals, Ann Arbour, MI, # 10010303). Briefly, the 100 μl sub-samples of the lipid-chloroform layer were thawed, and chloroform was evaporated using nitrogen gas (15 PSI). Samples were reconstituted with isopropanol, vortexed for 15 sec and incubated at room temperature for 1 hr. Ten microlitres of either TAG standard (0, 3.125, 6.25, 12.5, 25, 50, 100, 200 mg/dl) or sample were assayed in duplicate. Note that the standard was prepared with isopropanol. A chloroform blank, in which 100 μl chloroform was evaporated and reconstituted with isopropanol, was also used to ensure chloroform did not affect absorbance. Average absorbance was measured at 530 – 550 nm using a FLUOstart Omega multimode microplate reader (BMG Labtech, Ortenberg Germany). Final TAG values were reported in percent TAG of lipid (g TAG/g lipid*100). TAG samples from five fish were excluded from analyses (two from 7D group - one from week 4, one from week 5, two from 7D-fed group in week 9, and one that died during the experiment), as they developed a precipitate when added to the isopropanol and the solids interfered with absorbance, leading to an overestimate of TAG concentration.

4.3.7.5 Calculations

We calculated smolt condition parameters: Fulton's condition factor (K) was calculated using Equation 4.1:

$$K = \frac{Wt}{FL^3} * 100 \tag{4.1}$$

where weight Wt is in grams and fork length FL is in centimeters. The percent of whole body protein P was calculated from percentages of water W, lipids L and ash A (Hendry et al., 2000) using Equation 4.2:

$$P = 100 - (W + L + A) \tag{4.2}$$

Energy density (D; MJ/kg) can be calculated from the amount (g/kg) of lipid (l) and protein (p) using Equation 4.3:

$$D = l * 0.0362 + p * 0.0201 \tag{4.3}$$

where 0.0363 and 0.0201 are the energy densities of lipid and protein, respectively (Brett and Groves, 1979).

4.3.8 Statistical analyses

Survival analysis was used to compare prolonged swim performance or survival among the three treatment groups: 7D, 14D, 21D. Failure time, or survival analysis, is used to compare groups of right-censored data (Therneau and Grambsch, 2000). Swim trials were a form of right-censored data, as trials were ended after 90 min and thus a fish could have continued to swim for one minute or several more hours and this information was lost. A Cox proportional hazards model was used to determine significance of the effect of treatment group on swim time or survival. Analysis of variance was used to compare each physical variable (i.e., fork length, weight, and condition factor) across 7D, 14D, and 21D treatment groups to determine if variables differed across groups. Bonferroni pairwise tests were used to compare physical and energetic condition variables between fish that were dead or alive at the end of the survival experiment (Table 4.7). We calculated a Bonferroni correction (0.05/8 tests) and applied a significance level of $\alpha = 0.00625$.

We used generalized linear models to test specific hypotheses of the relationship between energetics and swim performance and survival. Use of a generalized linear model resulted in some loss of data precision (data were compressed to either 'completed' trial (finished 90 min swim trial) or 'failed' trial (swam for less than 90 min of swim trial), resulting in loss of individual swim time), at the benefit of using a model that has an established method for use in prediction. We used a generalized linear modelling approach, fit with a binomial distribution and a logit link function, to compare models of different correlated smolt condition variables and determine the most parsimonious models of swimming success/survival. No

random effect was used as the number of fish that completed the swim trial was very small in some weeks, which prevented convergence. However, top model residuals were examined for patterns among rearing tanks and weeks, and none were found, suggesting tank and week did not affect model output (Figs. 4.8, 4.9). For the swim performance model, we used energetic correlates from the 7D group only, since swim performance for the 7D, 14D, and 21D groups did not differ. Therefore, we compared eight individual-level variables for the 7D group (i.e., weight, length, condition factor, energy density, percent lipid, percent water, percent protein, and TAG) in 16 models (Table 4.2). For the survival model, we used energetic variables from all three groups combined, and compared 16 models, as with the swim performance model (Table 4.3). All variable combinations, except those that were highly correlated (correlation coefficient >0.6; Fig. 4.10) or not independent (i.e., energy density was not independent for lipid or protein content, since it is calculated from lipid and protein content) were used in models. All variables were standardized and centered. Model comparison was completed using Akaike Information Criterion corrected for small sample sizes (AIC_c), where models with <2 ΔAIC were considered most parsimonious (Burnham and Anderson, 2002). The top swim performance model was validated using k-fold validation, whereby the model was re-parameterized with 90% of the data (training dataset) and used to predict remaining 10% of data (test dataset). Predicted probabilities of $\geq$0.5 were considered to have completed the swim test and <0.5 were considered to have failed the swim test. Predictions were compared to observations to determine model predictive performance. This procedure was repeated 1000 times with samples randomly assigned to either training or test datasets. All statistics were performed in R statistical computing environment (v 3.5.2, R Core Team, 2018) using RStudio GUI (v1.1.463, 2018) and the following packages `AICcmodavg` (Mazerolle, 2017), `lme4` (Bates et al., 2015), `survival` (Therneau, 2015) and `coxme` (Therneau, 2020), and graphing was done with `ggplot2` (Wickham, 2009).

4.4 Results

4.4.1 Food deprivation and individual attributes

Wild sockeye salmon smolts kept for up to 61 days without food decreased in condition factor, energy density, and lipid and protein content, and increased in water content throughout the period of food deprivation. Between collection in the river and termination of the experiment (61 days), smolts (both alive and dead at the end of the experiment) lost an average of 1.74 g (35% of initial body weight), resulting in a 28% decrease in Fulton's condition factor (K) (0.74 to 0.53) and a 34% decrease in energy density (4.29 MJ/kg to 2.83 MJ/kg). Lipid values decreased on average from 2.88% to 1.49%, and protein content decreased from 16.14% to 11.41%. TAG did not change, shifting from 25% of lipid to 22% of lipid.

Shifts in body energy metrics and condition factor were due to the experimental treatments of food deprivation rather than an artifact of holding, given that fish condition metrics

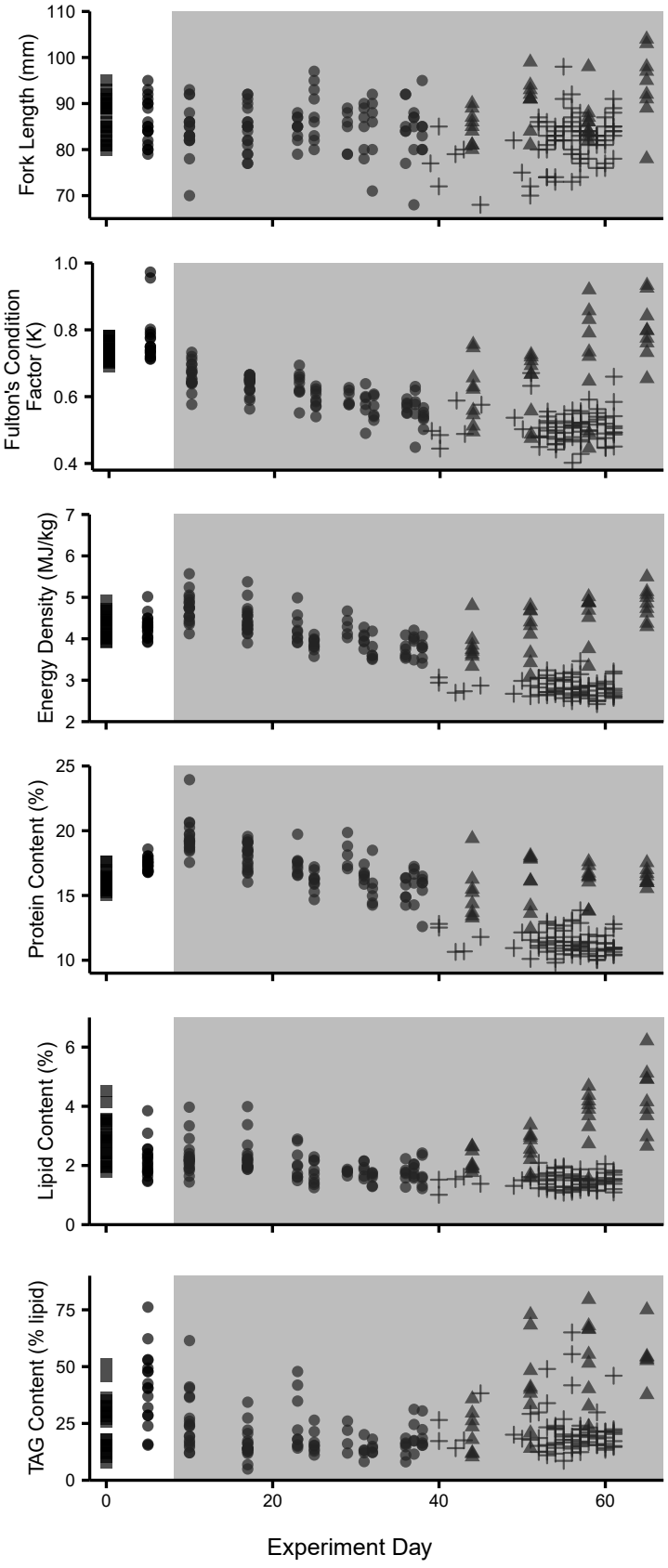

Figure 4.2: Physical and energetic condition variables changed throughout the holding period for individuals that were measured immediately after being caught (square), held without food and alive (7D group only; closed circle), held without food and died (all treatment groups; cross), fed after 28 days of starvation (7D-fed group; triangle). Non-shaded region represents fish sampled in freshwater, shaded region represents fish held in saltwater. Generally, condition metrics decreased through time for food deprived fish. Protein content and energy density (calculated from protein and lipid content) increased after transfer to saltwater, likely due to short term dehydration during the physiologic transition to life in seawater.

returned to pre-experiment levels within three to four weeks for the 7D-fed group that were food deprived for 28 days (Fig. 4.2). Over the 28 days of re-feeding, 7D-fed fish almost doubled their initial average weight of 3.63 g in week 5, growing to an average of 6.89 g, and had begun to grow in length (~10 mm), which led to a 60% increase in Fulton's condition factor (0.5 to 0.8). Fish also recovered energetic condition with a 20% increase in energy density (4.00 MJ/kg to 4.84 MJ/kg) due to an increase in lipid content (1.77% to 4.28%), as protein content stayed relatively stable. TAG levels also increased from 15% in week 5 at the start of feeding to 54% TAG of lipid (Table 4.6).

4.4.2 Experiment 1: migration duration and swim performance/survival

Swim performance decreased equally for all unfed groups with >80% of fish not being able to finish the swim test after greater than four weeks of food deprivation (based on 283 fish in 32 trials). Twenty-one smolts (7.4%) would not swim in the flume, instead falling to the back of the flume and remaining there during the acclimation period (Table 4.5). These fish were removed from the study. Fish that were included in the swim trials swam actively in the flow, and generally did not exhibit any 'cheating' behaviours such as swimming near the front of the flume where current was more irregular or drifting behind another fish. More fish completed the trial in week one (83%), compared to week six (12%)(Figs. 4.3, 4.4). When swim performance was compared across the three treatment groups (timing of switch to saltwater) using Cox proportional hazards (weeks 2 – 6, week one was not included in this analysis), the hazard rate (i.e., effect size) was not significantly affected by group (Wald test, 1.35, df = 2, p = 0.5). Swim trials were terminated in week six, because the swimming endpoint had been exceeded (more than two successive weeks where >80% of fish failed the trial). Fish were held for an additional three weeks, until half of the remaining fish had died (50% mortality, survival endpoint). There were no differences in mortality across all three groups (Wald test, 1.92, df = 2, p = 0.4). Despite a decrease in overall physical and energetic condition no mortalities occurred during or close to the transfer of smolts to saltwater. Groups did not differ in fork length (ANOVA, df = 2, F value = 0.895, p = 0.41) and weight (ANOVA, df = 2, F value = 2.956, p = 0.05).

4.4.3 Experiment 2: prolonged swimming and condition

Concomitant with a decrease in swim performance, condition decreased throughout the swim trials. Since swim performance did not differ among groups, we determined the relationship between swim performance and condition metrics using data from the 7D group (7D, n = 108; Table 4.5). Over the six weeks that the swim trials were completed, smolts from the 7D transfer group lost an average of 1.25 g (25% of initial body weight), resulting in a 26% decrease in Fulton's condition factor (K) (0.77 to 0.57) and 11% decrease in energy density (4.29 MJ/kg to 3.83 MJ/kg). Lipid values decreased on average from 2.20% to

Table 4.1: Changes in sockeye salmon smolt morphometrics, energy density, and proximate body constituents during the experiment for fish collected at Chilko River sampling site, for fish from the 7-day saltwater transfer group, and for fish that had died during the experiment.

	River Sampling	Week 1		Week 2[1]		Week 3		Week 4		Week 5		Week 6		Deaths[2]
Completed Trial? (Y/N)	NA	Y	N	Y	N	Y	N	Y	N	Y	N	Y	N	NA
Sample Size	20	3	15	11	7	9	6	13	2	16	1	13	1	78
Fork Length (mm)	87.2	83.0	86.7	82.5	87.3	84.4	84.0	86.9	86.0	85.2	88.0	86.4	85.0	81.8
(SE)	±0.94	±1.53	±1.31	±1.63	±1.51	±1.54	±2.37	±1.56	±1.00	±1.15		±1.25	±0.59	
Weight (g)	4.91	4.84	4.97	3.72	4.55	3.86	3.82	3.97	4.31	3.63	4.14	3.68	3.87	2.81
(SE)	±0.15	±0.09	±0.22	±0.23	±0.26	±0.25	±0.34	±0.21	±0.26	±0.17		±0.16		±0.06
Fulton's Condition Factor	0.74	0.85	0.76	0.65	0.68	0.63	0.64	0.60	0.68	0.58	0.61	0.57	0.63	0.51
(SE)	±0.01	±0.06	±0.02	±0.01	±0.01	±0.01	±0.01	±0.01	±0.17	±0.01		±0.01		±0.01
Energy Density (MJ/kg)	4.29	4.39	4.27	4.85	4.60	4.44	4.49	3.96	4.37	4.00	4.18	3.83	4.00	2.82
(SE)	±0.06	±0.06	±0.08	±0.12	±0.07	±0.09	±0.21	±0.06	±0.20	±0.08		±0.06		±0.02
Water(% wet weight)	78.77	77.89	77.92	74.62	75.48	76.39	76.34	78.51	77.20	77.82	76.74	78.49	77.87	82.96
(SE)	±0.20	±0.24	±0.27	±0.57	±0.33	±0.42	±0.70	±0.25	±0.29	±0.41		±0.25		±0.15
Protein (% wet weight)	16.14	17.12	17.49	19.68	19.22	18.13	17.91	16.40	17.59	16.76	18.49	15.86	17.05	11.32
(SE)	±0.15	±0.17	±0.14	±0.49	±0.29	±0.31	±0.56	±0.23	±0.04	±0.36		±0.22		±0.10
Lipid (% wet weight)	2.88	2.62	2.09	2.46	2.04	2.21	2.45	1.84	2.31	1.77	1.29	1.78	1.57	1.49
(SE)	±0.16	±0.25	±0.15	±0.21	±0.11	±0.15	±0.32	±0.10	±0.58	±0.05		±0.09		±0.03
TAG (% lipid)	24.9	46.7	39.6	28.8	21.8	17.4	14.2	16.9	41.3[3]	15.1[3]	NA[3]	16.9[3]	24.6	21.1[3]
(SE)	±2.6	±9.8	±4.3	±4.3	±3.6	±1.7	±4.3	±1.3	±6.5	±1.3		±1.4		±1.1

[1] Fish were transferred to saltwater 3 days before Week 2 sampling/swim performance trials.
[2] Deaths that occurred before survival endpoint was reached.
[3] One triglyceride (TAG) sample was removed because a precipitate formed, thus TAG was calculated from a n-1 sample size for that group.

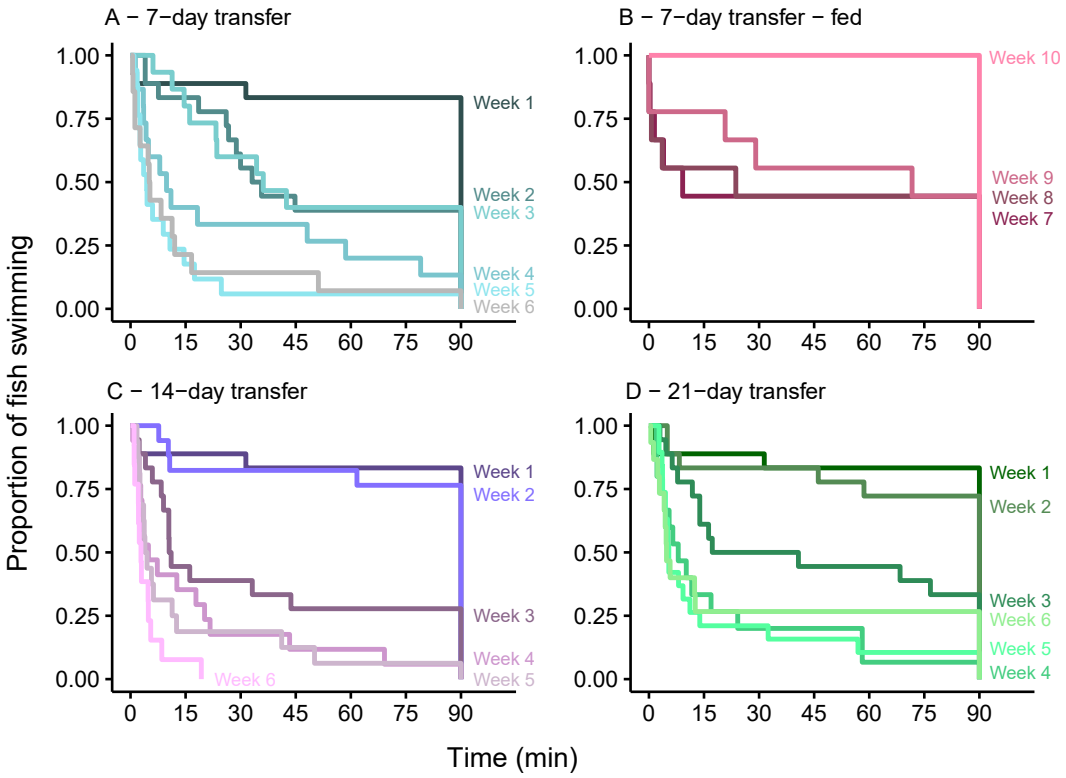

Figure 4.3: Swim performance (time swimming up to 90 min) of fish held without food and transferred to saltwater after A) 7 days, C) 14 days, D) 21 days; and B) fish that were transferred to saltwater after 7 days, food deprived for 28 days before beginning feeding in week 5 such that week 7 represents two weeks of feeding, week 8 represents three weeks of feeding and so forth. Each shade of a colour represents a week of swim trials which were conducted weekly.

1.74%, protein from 17.42% to 15.94% and TAG from 41% of lipid to 17% of lipid (Tables 4.1, 4.8).

Grouped across weeks, fish that completed the swim test had 14% higher condition factor (0.71 complete vs. 0.61 incomplete), higher energy density (4.39 MJ/kg complete vs. 4.20 MJ/kg incomplete) and higher protein, lipid, and TAG content, compared to those that could not complete the swim test (Fig. 4.5). We compared generalized linear models using AIC_c to determine which set of energetic variables best predicted whether fish completed the 90 min swim test or failed the test (stopped swimming before 90 min) (Tables 4.2, 4.4). Energetic variables were highly correlated (Fig. 4.10). We found that the most parsimonious model predicting completion of the swim test included only condition factor as a predictor variable ($\Delta AIC < 2$; Fig. 4.6, Left). This model was followed by one that included condition factor and TAG ($\Delta AIC = 2.06$). We used k-fold model validation to determine that the top

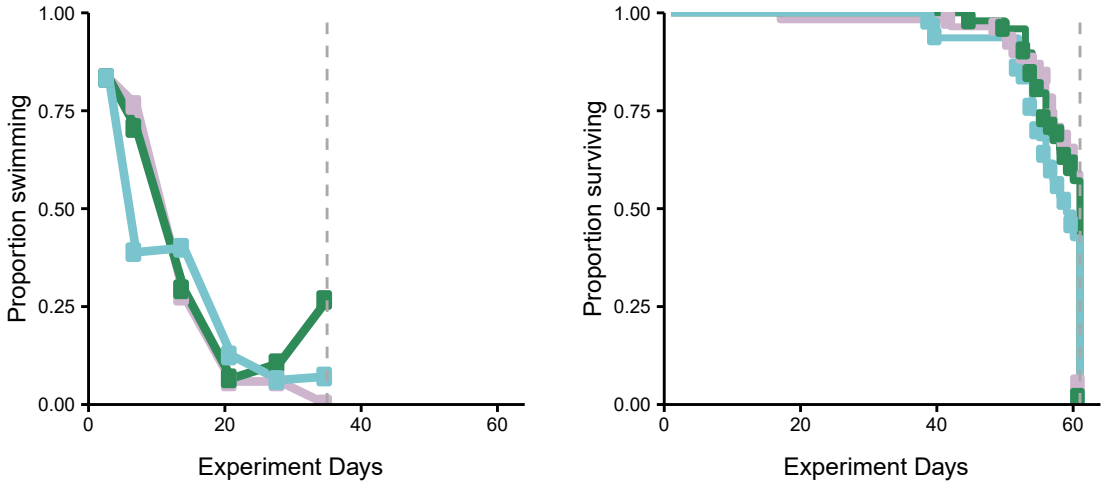

Figure 4.4: Weekly proportion of food-deprived fish that completed the 90 min swim trial (left) or survived (right) for each treatment group, transferred to saltwater after: 7 days (blue), 14 days (light purple), and 21 days (green). Grey vertical line represents the end of the testing/observation period. Observation periods ended after >80% of the fish could not finish the test for over two weeks (left) and after 50% of fish had died (right).

model accurately predicted whether a fish would pass or fail the swim test ~79.5% of the time.

Swim performance rebounded in 7D-fed group confirming that the manipulation of energy levels was the determinant of changes in swim performance. When fed for 21 days, subsequent to 28 days of food deprivation, swim performance increased (57% percent of fish finished the swim trial after three weeks of feeding); however, swim performance did not immediately return to pre-starvation levels. It took ~3 weeks of feeding for energetic correlates to return to or increase above capture levels, suggesting some effects of either holding or legacy effects from starvation (Table 4.6). After 35 days (week 10) of feeding 100% of fish completed the test, however fish had begun growing which could have affected the results of the test (Fig. 4.3, Table 4.6).

4.4.4 Experiment 3: survival and condition

Mortality during the 61-day holding period was biased towards the end of the experimental period, with the majority of fish dying in the last 10 days of the experiment. At the termination of the survival experiment, 78 fish had died, while 72 fish remained alive and were euthanized. Fish that remained alive at the end of the experiment were slightly larger than fish that died during the experiment (FL = 86.3 mm vs. 81.8 mm and weight = 3.58 g vs. 2.81 g, respectively; Bonferroni t test, p>0.0001; Table 4.7, Fig. 4.11). Energy density and proximate body constituents were not markedly different. Fish at the end of the experiment

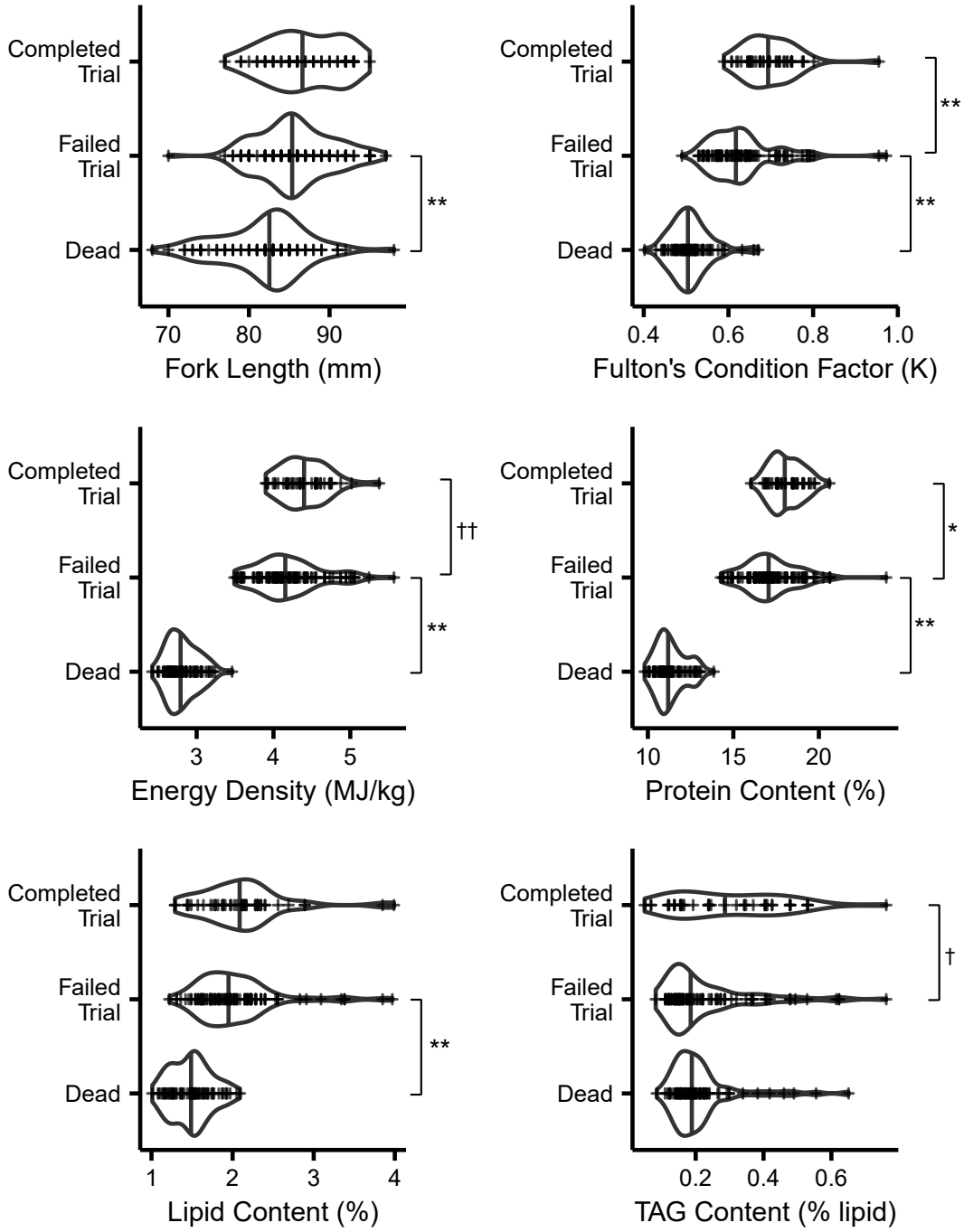

Figure 4.5: Swim performance and survival by energetic correlates for starved fish. Completed – fish that finished the 90 min swim; Failed – fish that did not complete the 90 min swim; and Dead – fish that died during the survival experiment. This analysis groups all weeks of swimming together. Significance of post hoc Bonferroni pairwise tests are indicated by either $p \leq 0.05$ (†), $p \leq 0.01$ (††), $p \leq 0.001$ (*), or $p \leq 0.0001$(**).

Table 4.2: Model comparison of generalized linear models predicting swim success/failure for 7D group.

	K	Log Likelihood	ΔAIC	ωAIC
Condition Factor	2	-44.07	0.00	0.71
Condition Factor + TAG	3	-44.03	2.06	0.25
TAG + Weight	3	-46.14	6.27	0.03
Weight	2	-48.83	9.52	0.01
TAG + FL	3	-51.38	16.76	0.00
TAG	2	-52.48	16.82	0.00
Protein Content + FL	3	-53.83	21.67	0.00
Energy Density + FL	3	-53.89	21.77	0.00
Protein Content	2	-55.25	22.37	0.00
Energy Density	2	-55.32	22.50	0.00
Intercept	1	-57.29	24.34	0.00
Lipid Content	2	-56.65	25.16	0.00
FL	2	-56.68	25.21	0.00
Lipid Content + FL	3	-55.78	25.55	0.00
Moisture Content	2	-56.98	25.82	0.00
Moisture Content + FL	3	-55.97	25.93	0.00

FL = fork length (mm), TAG = percent triglycerides of lipid, ΔAIC = difference in AIC between models, ωAIC = Akaike weight of model. Fork length, weight, and Fulton's condition factor were determined from fish before they were frozen; n = 90.

were likely close to death, which makes it difficult to compare energy metrics between those alive or dead at the termination of the experiment. Therefore, it is more useful to compare the condition of fish that failed to swim (i.e., fish that could not complete the swim trial, but were still alive at the swim performance endpoint) and fish that died by the end of the experiment (Table 4.1). Energy density and protein content values between fish that failed the swim trial and fish that died during the experiment separated nearly completely (did not overlap), thus linear models with these covariates predicted perfectly (Fig. 4.6), and were the best fit models (Tables 4.3, 4.4). For example, the range of energy density values for dead fish was 2.40 – 3.46 MJ/kg, whereas the range of values for a fish that did not swim was 3.49 – 5.57 MJ/kg. Similarly, the range of protein for fish that died before the end of the experiment was 9.36 – 14.13% and 14.27 – 23.94% for fish that failed to swim. Thus, thresholds for fish surviving based on energy density and/or protein were 3.47 MJ/kg and 14.20%.

Table 4.3: Model comparison for generalized linear models predicting swim failure/death for all treatment groups combined.

	K	Log Likelihood	ΔAIC	ωAIC
Energy Density	2	0.00[1]	0.00	0.37
Protein Content	2	0.00[1]	0.00	0.37
Protein Content + FL	3	0.00[1]	2.09	0.13
Energy Density + FL	3	0.00[1]	2.09	0.13
Moisture Content	2	-4.70	9.39	0.00
Moisture Content + FL	3	-4.64	11.38	0.00
Lipid Content	2	-59.93	119.87	0.00
Lipid Content + FL	3	-59.86	121.82	0.00
Condition Factor + TAG	3	-68.84	139.80	0.00
Condition Factor	2	-76.52	153.04	0.00
TAG + FL	3	-81.48	165.07	0.00
TAG	2	-83.33	166.67	0.00
TAG + Weight	3	-82.85	167.82	0.00
Weight	2	-90.46	180.91	0.00
Intercept	1	-91.73	181.40	0.00
FL	2	-90.84	181.67	0.00

[1] Energy density and protein content of fish separate perfectly allowing for probabilities of 0 or 1. As a result model estimates of confidence intervals approach infinity.
FL = fork length (mm), TAG = percent triglycerides of lipid, ΔAIC = difference in AIC between models, ωAIC = Akaike weight of model. Fork length, weight, and Fulton's condition factor were determined from fish before they were frozen; n = 133.

Table 4.4: Top model parameter coefficients for generalized linear models predicting swim success/failure and swim failure/death.

Top Model	Parameter	Coefficient (95% Confidence Interval)
(success/failure) = Condition Factor		
	Intercept	-1.62
		(-2.38, -0.97)
	Condition Factor	1.68
		(0.95, 2.56)
(swim failure/death) = Energy Density		
	Intercept	-1299[1]
	Energy Density	379[1]
(swim failure/death) = Protein Content		
	Intercept	-4601[1]
	Protein Content	324.1[1]

[1] Energy density and protein content of fish separated perfectly allowing for probabilities of 0 or 1. As a result model estimates of confidence intervals approach infinity.

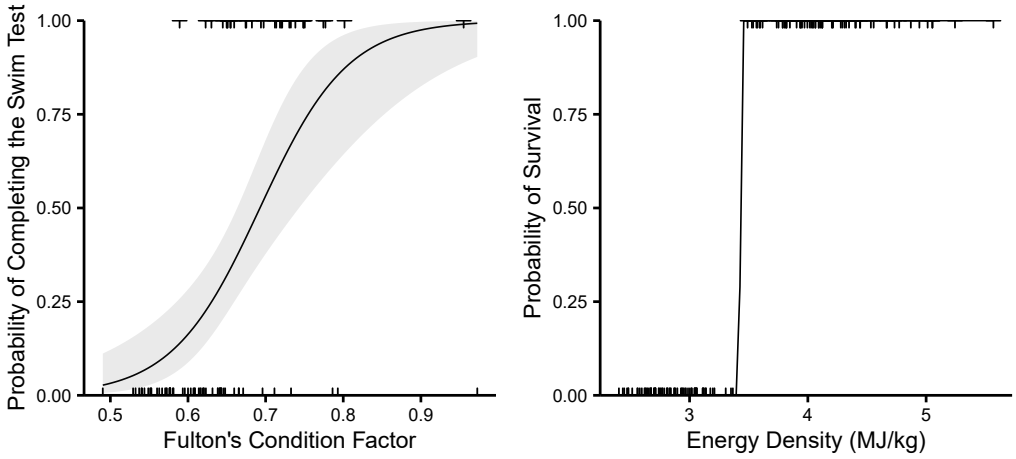

Figure 4.6: Top model predicted probabilities of 7D fish completing the swim trial (1 = complete, 0 = incomplete; left) and top model predicted probabilities of fish failing the swim test (1) or dying (0) for all un-fed groups (right). Grey shaded regions represent 95% confidence regions.

4.5 Discussion

We held sockeye salmon smolts for 61 days during which we observed swim performance and survival and found that a continuous decline in condition factor was predictive of swim performance, while a threshold existed between energy density/protein content and survival. We chose two experimental endpoints (swim performance: 80% of fish could not finish the first test, survival: 50% of the fish had died) to represent both a biologically relevant and more clinical endpoint, respectively. The first endpoint, a lack of swimming capacity, represents a more ecologically relevant endpoint than a clinical diagnosis of death because fish with decreased swim performance likely have a higher probability of being predated (Plaut, 2001). The second endpoint can be used to compare with other starvation studies and represents a 'true' clinical endpoint, where outside of external factors such as predation, a fish would die. There was no difference in swim performance or survival between treatment groups (7D, 14D, 21D) suggesting that freshwater migration duration did not influence these two metrics. Using swim performance data from the 7D group as a response variable and physical or energetic condition predictor variables in a generalised linear model framework, we found that Fulton's condition factor was the best predictor variable of the swim performance endpoint. Indeed, k-fold validation indicated that using Fulton's condition factor alone could predict whether a fish could successfully complete a 90-min prolonged swim trial 79.5% of the time. We also compared the group of fish that could not finish the swim trial to the group of fish that died and found an energy density threshold of 3.47 MJ/kg below which a fish will die. The swim performance endpoint was

reached at higher energy levels, and well before the survival endpoint was reached. The swim performance endpoint was observed in individuals with energy levels close to the lowest levels observed in natural systems (Rondorf et al. 1985, D. Patterson, pers. comm.), indicating that swim performance, and therefore condition factor, may be a more accurate representation of survival estimates in natural populations.

Contrary to our prediction, condition factor, rather than energetic variables, was the best predictor of swim performance. Swim performance decreased as condition factor decreased. It is possible that longer fish could have had an advantage in the swim flume compared to shorter fish, as the swim tunnel had a static flow, thus making shorter fish work proportionally harder in the flume (see Beamish 1978; Simpkins et al. 2004). However, we saw no evidence that length influenced the results of the test, only condition factor. Length and condition factor are low effort, low cost, and non-lethally collected variables which are often measured in field studies and have been related to smolt survival (Healey, 1982; Ward et al., 1989; Henderson and Cass, 1991; Duffy and Beauchamp, 2011). This is not the first study to find that condition factor rather than energetic variables or metabolites better predicted swim performance in fishes (Atlantic cod (*Gadus morhua*): Martinez 2003; largemouth bass (*Micropterus salmoides*): Gingerich et al. 2010; gilthead seabream (*Sparus aurata*): Faria et al. 2011). Here we demonstrate this relationship in salmon smolts. Interestingly, TAG was not the best predictor of either swim performance or survival, and in fact, appeared stable throughout the experiment. Energy density (energy from lipid and protein) and lipid content have been related to survival in salmon and other species (LeBrasseur, 1969; Simpkins et al., 2003, 2004; Ferguson et al., 2010), and since TAG is a non-structural lipid, we predicted that this variable would better predict survival compared to lipid content. However, energy density and protein content were most distinct between the fish that failed the swim test and the fish that died, rather than lipid or TAG. The importance of energy density, rather than lipid content, is likely due to the inter-individual variance in use of protein and lipid as energy storage (McCue, 2010). It is also possible that variables other than what we measured could have better predicted swim performance and/or survival. For example, metabolic rate, metabolic enzymes, organ mass (e.g., liver somatic index), and glycogen have been correlated with condition and performance (Martinez, 2003, 2004; Gingerich et al., 2010). However, in these previous studies the fish were not starved, and the utility of these measurements likely changes during starvation (McCue, 2010). Alternatively, fatty acids could be correlated with performance as Pierce et al. (2005) found that dietary fatty acid influenced performance in a migratory bird. Thus, future research could clarify the roles of different components of energy stores in performance and survival.

Energy values observed in our experiment were similar to what has been observed in natural systems and other studies. The median lipid content for those that failed the trial was 1.93%, approaching values previously estimated to be the lower threshold for survival in the wild (DFO, unpublished data). Indeed, wild sockeye salmon smolts have rarely been

found in the wild with lipid values lower than 2.0% or condition factors less than 0.57 (DFO, unpublished data). This study examined fish just prior to migration, and so likely represents fish with reserved energy for migration. Rondorf et al. (1985) found that lipid values approached 1.4% and energy density decreased to 1.02 Kcal/g (4.27 MJ/kg) for hatchery origin Columbia River Chinook salmon smolts nearing the estuary after completion of freshwater migration. The energy density values found in their study fall close to the group of fish that did not complete the swim trial in our experiment, whereas the lipid values fall closer to those that died during our experiment. Persson et al. (2018) found a threshold for survival of 3.5 MJ/kg and condition factor of 0.65 in starved Atlantic salmon (*Salmo salar*) smolts, consistent with our findings. Another study held juvenile chum salmon *(O. keta)* captured in the Icy Strait, Alaska, USA, without food for 45 days in saline water in living-stream tanks and found that energy density (determined using a bomb calorimeter) decreased to ~650 cal/g (2.72 MJ/kg) (Ferguson et al., 2010), similar to the lowest energy densities measured in fish held for 61 days in our experiment. At the end of our experiment, surviving fish were longer than dead fish (Fig. 4.7), which is consistent with Simpkins et al. (2004) who found that for sedentary fish held without food, smaller fish died before larger fish, perhaps due to decreased lipid stores. Together with the swimming results, this suggests that smaller, lower condition fish might be more likely to die under conditions of starvation (Biro et al., 2004). Furthermore, these examples could represent species- or population-specific differences in physiological response to starvation. Indeed, swim performance differs across populations of fed coho (*O. kisutch*) and sockeye salmon (Taylor and McPhail, 1985; Eliason et al., 2017). However, our findings that fish with energy densities of <3.47 MJ/kg are unlikely to survive appear consistent with other literature (Rondorf et al., 1985; Persson et al., 2018).

Food-deprived fish held in the lab setting likely lost energy more slowly than non-feeding fish that would be actively migrating. Fish have very low resting metabolic rates (10 to 30 times less than mammals and up to 100 times less than birds of the same weight), such that the majority of energy is spent on locomotion (Brett, 1972). Fish held in the lab moved very little, and thus likely spent much less energy per unit time than an actively foraging or migrating fish. In fact, Rondorf et al. (1985) found that salmon smolts held in the lab lost about 15% body lipids versus 65% in fish that had been released and were actively migrating over the same period. In a more recent study of hatchery-origin rainbow trout (*O. mykiss*), sedentary fish (held in tanks with no directional current) had percent lipid values that averaged 3.5% higher than active fish (in tanks with directed current, forcing fish to swim) held without food for the same period of time (Simpkins et al., 2003). Therefore, caution needs to be taken when considering the real-world application of our lab-based longevity estimates. Hence, our finding of an 80% failure rate after four weeks of starvation is likely a substantial overestimate compared to what would be observed in natural settings, with actual time to 80% failure being much less than four weeks, depending

on water temperature. Similarly, we would expect that fish in a natural setting would likely die much earlier than the 51 – 61 days in which we observed the majority of mortality in our experiment. Longevity in the natural environment is likely less than the 3 – 6 weeks in which we observed fish complete swim trials, yet juvenile salmon migrations in altered rivers can take over two weeks to complete (Giorgi et al., 1997; Smith et al., 2002).

Both aerobic prolonged swim performance and anaerobic burst swim performance are likely related to the ability to capture prey, escape predators, and migrate (Plaut, 2001). We measured prolonged swim performance, as an indicator of endurance, and found a marked decrease during starvation that is consistent with existing literature (Martinez, 2003) and with our original hypothesis. Decreased metabolic and contractile capabilities of fish muscle tissue during starvation was the likely underlying mechanism for the observed decrease in swim performance (Moon and Johnston, 1980; Sullivan and Somero, 1983; Black and Love, 1986; Kiessling et al., 1990; Martinez, 2003). An additional component of swim performance that was not measured was anaerobic (burst) swim performance, which is used to quickly escape from predators or capture prey. Existing literature suggests that anaerobic swim performance may be more impacted than aerobic performance during starvation (Beardall and Johnston, 1983; Lowery and Somero, 1990; Martinez, 2004), and thus represents a future avenue for research. Therefore, aerobic swim performance, as measured in this study, represents a conservative indicator of the response to a decrease in condition.

Our study is one of a few studies that examines swim performance and survival in a wild fish. Others have used hatchery fish, due to their availability and readiness to live in aquaculture facilities. However, swim performance of hatchery fish can be much lower than that of wild fish (Bams, 1967; Beamish, 1978; McDonald et al., 1998; Simpkins et al., 2003, 2004; Pedersen et al., 2008). For example, we used the same apparatus as Collins et al. (2013), which examined prolonged swim performance of hatchery-reared sockeye salmon. The majority of fish in their experiment tired by 20 min; however, we required a 90 min swim to achieve variability in swim performance in the first week of the swim trials. McDonald et al. (1998) made a similar observation when they compared swim performance of hatchery reared and wild Atlantic salmon. Wild fish had better fin quality, higher anaerobic capacity, and higher swim endurance than hatchery fish (McDonald et al., 1998). Hatchery fish may differ from wild fish which makes it challenging to draw conclusions about swim performance of wild fish and velocity barriers in natural systems, using hatchery-reared fish (McDonald et al., 1998).

Understanding condition-dependent swim performance and survival could help elucidate carry-over effects and limits on survival during seaward and early marine migration in Pacific salmon. Survival through the early marine life history stage is size-, and likely condition-dependent, as juvenile salmon must grow quickly to escape gape-limited predators and expand prey options (Pope et al., 1994). Schooling behaviours may decrease predation risk through 'predator swamping', but these schooling behaviours require some level of

swim performance (Furey et al., 2021). In fact, predation may be condition-dependent, where lower conditions individuals are preferentially predated (Tucker et al., 2016). Thus, condition-dependent swim performance relationships could help predict probability of survival in natural systems. Additionally, most of the freshwater migration and some fraction of the marine migration corridor is food-limited (McKinnell et al., 2014), and therefore condition-dependent swim performance and survival relationships could clarify individual and population-level sensitivity to starvation.

Using wild salmon smolts and an experimental approach, we have developed a model to predict swim performance given condition factor. Condition factor is a simple and inexpensive tool that represents a likely avenue for measuring swim performance and thus survival probability. Indeed, prolonged swim performance collapsed three weeks prior to and at higher energy levels than the onset of mortalities. Survival was better predicted by energy density and protein content than condition factor. Energy density is a more clinical predictor of survival and is a more labour intensive and expensive measurement and requires lethal sampling. Given that different individuals and populations of salmon have different energetic status and condition (MacDonald et al., 2019), or may use estuary stopover habitat for different durations (Moore et al., 2016), here we provide the foundation for understanding the impacts of this variation. This study offers a new tool for contextualizing population-specific sensitivity to changes in migratory conditions or pre-migratory conditioning phase.

4.6 Acknowledgements

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4.7 Supplemental materials

4.7.1 Supplemental tables

Table 4.5: Morphometrics and condition factor for sockeye salmon smolts from each treatment group swum each week in swim trials.

		Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
All							
	Sample Size[1]	18	NA	NA	NA	NA	NA
	Num. Did Not Swim	0	NA	NA	NA	NA	NA
	Fork Length (mm)	86.1±0.8	NA	NA	NA	NA	NA
	Weight (g)	4.95±0.13	NA	NA	NA	NA	NA
	Fulton's Condition Factor	0.77±0.01	NA	NA	NA	NA	NA
	Median Swim Time (min)	90.0	NA	NA	NA	NA	NA
	Percent Completed Swim (%)	83	NA	NA	NA	NA	NA
7D							
	Sample Size[1]	NA	18	15	15	17	14
	Num. Did Not Swim	NA	0	3	2	1	4
	Fork Length (mm)	NA	84.4±1.0	84.3±0.9	86.8±1.0	85.4±0.9	86.3±1.0
	Weight (g)	NA	4.04±0.16	3.85±0.15	4.01±0.13	3.66±0.13	3.69±0.13
	Fulton's Condition Factor	NA	0.66±0.01	0.63±0.01	0.61±0.01	0.58±0.01	0.57±0.01
	Median Swim Time (min)	NA	34.4	36.2	9.8	4.4	5.2
	Percent Completed Swim (%)	NA	39	40	13	6	7
14D							
	Sample Size[1]	NA	17	18	17	15	13
	Num. Did Not Swim	NA	0	0	1	0	4
	Fork Length (mm)	NA	86.1±1.0	86.1±1.2	84.3±1.0	86.6±1.1	83.6±1.5
	Weight (g)	NA	4.67±0.13	4.26±0.19	3.71±0.16	3.85±0.13	3.29±0.17
	Fulton's Condition Factor	NA	0.73±0.01	0.65±0.01	0.61±0.01	0.59±0.01	0.56±0.01
	Median Swim Time (min)	NA	90.0	10.8	4.9	3.9	2.9
	Percent Completed Swim (%)	NA	76	28	6	7	0
21D							
	Sample Size[1]	NA	18	18	15	19	15
	Num. Did Not Swim	NA	0	0	3	0	3
	Fork Length (mm)	NA	85.8±0.8	86.8±0.8	85.8±1.2	86.0±0.7	87.3±1.0
	Weight (g)	NA	4.65±0.12	4.52±0.10	3.84±0.16	3.80±0.11	3.91±0.16
	Fulton's Condition Factor	NA	0.73±0.01	0.69±0.01	0.60±0.01	0.59±0.01	0.58±0.01
	Median Swim Time (min)	NA	90.0	29.0	8.0	5.4	4.8
	Percent Completed Swim (%)	NA	72	33	7	11	27

[1] Sample size is the number of fish that swam in the study. Mean fork length, weight and Fulton's condition factor, and median swim time were calculated from fish that swam only. The fish that did not swim during the initial acclimation phase of the swim performance trial were removed from the study.
Light gray cells indicate values taken from fish that were in saltwater at the time of the swim trial.

Table 4.6: Changes in sockeye salmon smolt morphometrics, proximate body constituents, and energy density during experiment for fish from the 7-day saltwater transfer group that were fed after 28 days of food deprivation.

	Week 7[1]		Week 8		Week 9		Week 10	
Completed Trial? (Y/N)	N	Y	N	Y	N	Y	N	Y
Sample Size[2]	4	4	3	4	3	4	0	9
Fork Length (mm)	83.5	87.0	88.0	93.8	84.0	88.8	NA	94.1
(SE)	±2.0	±1.5	±3.5	±1.9	±1.2	±3.3		±2.6
Weight (g)	3.25	4.60	4.39	5.89	4.48	5.66	NA	6.89
(SE)	±0.24	±0.47	±0.72	±0.42	±0.30	±0.61		±0.71
Fulton's Condition Factor	0.56	0.70	0.63	0.71	0.76	0.80	NA	0.80
(SE)	±0.03	±0.04	±0.04	±0.01	±0.08	±0.03		±0.03
Energy Density (MJ/kg)	3.66	4.21	4.38	4.38	4.69	4.91	NA	4.84
(SE)	±0.04	±0.30	±0.36	±0.12	±0.10	±0.03		±0.13
Water(% wet weight)	80.07	77.88	77.57	77.70	76.69	76.24	NA	76.95
(SE)	±0.03	±1.29	±1.35	±0.49	±0.29	±0.25		±0.25
Protein (% wet weight)	14.13	17.04	16.50	17.02	16.42	16.95	NA	16.38
(SE)	±0.43	±1.29	±1.35	±0.49	±0.29	±0.25	NA	±0.25
Lipid (% wet weight)	2.27	2.16	2.93	2.65	3.85	4.16	NA	4.28
(SE)	±0.22	±0.16	±0.24	±0.20	±0.27	±0.23		±0.38
TAG (% lipid)	20.8	24.6	49.7	48.2	54.0	66.4	NA	54.4[3]
(SE)	±0.04	±0.06	±0.09	±0.09	±0.08	±0.06		±0.04

[1] Fish were fed starting experiment week 5, therefore week 7 represents 14 days of feeding, week 8 represents 21 days of feeding, week 9 represents 28 days of feeding and week 10 represents 35 days of feeding.
[2] Only counts fish that swam during experiment, some fish refused to swim in tunnel (1 in week 7, 2 in weeks 8 and 9) and were removed from experiment.
[3] Two triglyceride (TAG) samples were removed as a cloudy/precipitate had formed and lipid extraction could not be repeated.

Table 4.7: Physical and energetic condition of individuals that were either alive or dead at the end of the experiment.

	Dead during the experiment	Alive at the end of the experiment
Sample Size	78	72
Fork Length (mm)	81.8	**86.3**
(SE)	±0.6	±**0.5**
Weight (g)	2.81	**3.58**
(SE)	±0.06	±**0.07**
Fulton's Condition Factor	0.51	**0.55**
(SE)	±0.01	±**0.01**
Energy Density (MJ/kg)	2.82	2.85
(SE)	±0.02	±0.03
Water (% wet weight)	82.96	**83.54**
(SE)	±0.16	±**0.14**
Protein (% wet weight)	11.33	11.49
(SE)	±0.10	±0.13
Lipid (% wet weight)	1.49	1.49
(SE)	±0.03	±0.02
TAG (% lipid)	21.1	22.7
(SE)	±1.1	±1.1

Bold values indicate statistical difference (pairwise Bonferroni t-test) between dead and alive at the end of the experiment at α=0.00625, adjusted for increased rate of false positives associated with multiple statistical tests.

Table 4.8: P values of pairwise tests between condition at capture and condition during subsequent periods of the experiment.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	End of Experiment (alive and dead)
Fork Length (mm)	1.0	1.0	1.0	1.0	1.0	1.0	0.01
Weight (g)	1.0	1.0	0.08	**0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Fulton's Condition Factor	1.0	1.0	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Energy Density (MJ/kg)	1.0	**0.002**	1.0	1.0	0.4	**0.0004**	**<0.0001**
Water (% wet weight)	1.0	**<0.0001**	**<0.0001**	1.0	1.0	1.0	**<0.0001**
Protein (% wet weight)	0.02	**<0.0001**	**<0.0001**	1.0	1.0	1.0	**<0.0001**
Lipid (% wet weight)	0.01	0.9	0.08	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
TAG (% lipid)	**0.0005**	1.0	0.5	1.0	0.6	1.0	0.2

Bold values indicate statistical difference (pairwise Bonferroni t-test) at α=0.00625, adjusted for increased false positive errors associated with multiple statistical tests.

Table 4.9: P values of pairwise tests between condition at the start of feeding (Week 5) and condition during subsequent periods of the experiment for 7D-fed fish.

	Week 7	Week 8	Week 9	Week 10
Fork Length (mm)	1.0	0.1	1.0	**0.0013**
Weight (g)	1.0	0.1	0.2	**<0.0001**
Fulton's Condition Factor	1.0	0.7	**0.002**	**<0.0001**
Energy Density (MJ/kg)	1.0	0.7	**0.002**	**<0.0001**
Water (% wet weight)	1.0	1.0	0.3	0.06
Protein (% wet weight)	1.0	1.0	1.0	1.0
Lipid (% wet weight)	1.0	0.1	**<0.0001**	**<0.0001**
TAG (% lipid)	1.0	**0.0007**	**<0.0001**	**<0.0001**

Bold values indicate statistical difference (pairwise Bonferroni t-test) at α=0.00625, adjusted for increased false positive errors associated with multiple statistical tests.

4.7.2 Supplemental figures

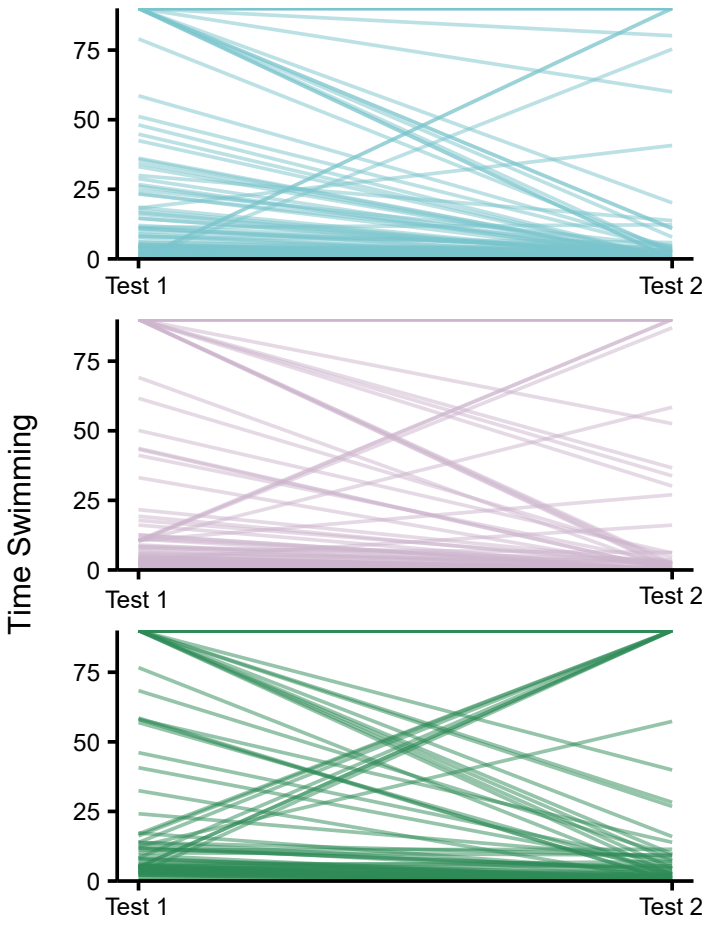

Figure 4.7: Repeatability of swim performance tests for all non-fed groups (7-day transfer (blue; top), 14-day transfer (light purple; middle), and 21-day transfer to saltwater (green; bottom)). Generally, fish swam for less time in test 2 than in test 1.

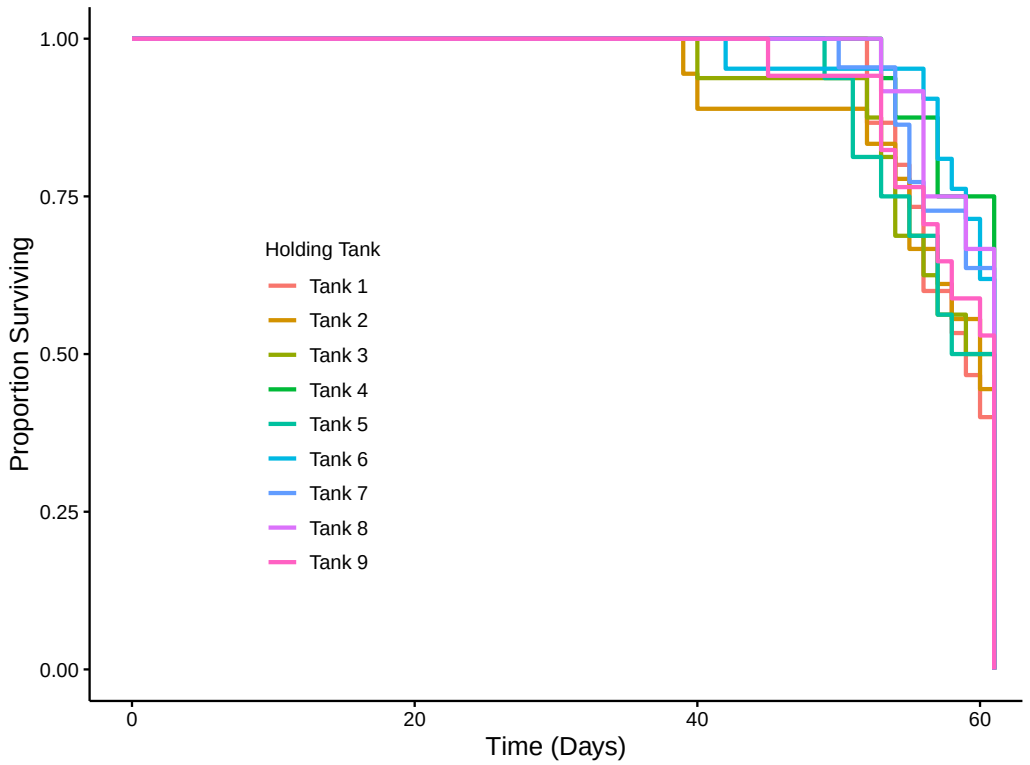

Figure 4.8: Survival curve for fish, broken down by holding tank. Fish were transferred to saltwater 7 days (holding tanks 1,2,3), 14 days (holding tanks 4,5,6), and 21 days (holding tanks 7,8,9) after emigration from their rearing lake.

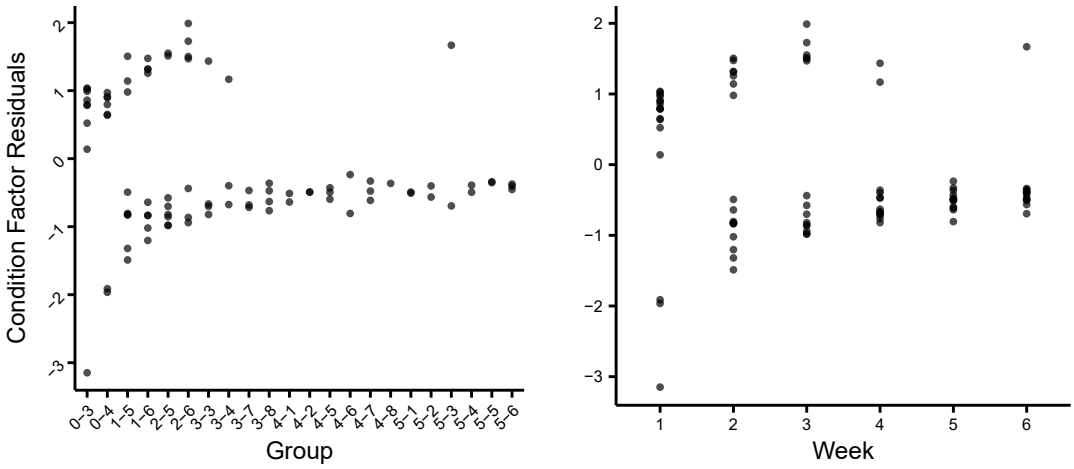

Figure 4.9: Residuals from the generalized linear model predicting completion or failure of the swim test using condition factor compared to swim group or experimental week. Due to limited number of individuals that completed swim tests in later weeks, group and week could not be added as a random effect. Here we demonstrate that there is no clear pattern in residuals across groups and weeks of the experiment. Group designation is indicated by 'week'-'trial group', where trial group was designated between 1 – 6, and week was designated between 0 – 5. We completed ANOVAs comparing condition factor residuals and either group or week and found no significant effect of either (Group, df = 21, F value = 0.531, p = 0.947; Week, df = 5, F value = 1.325, p = 0.262).

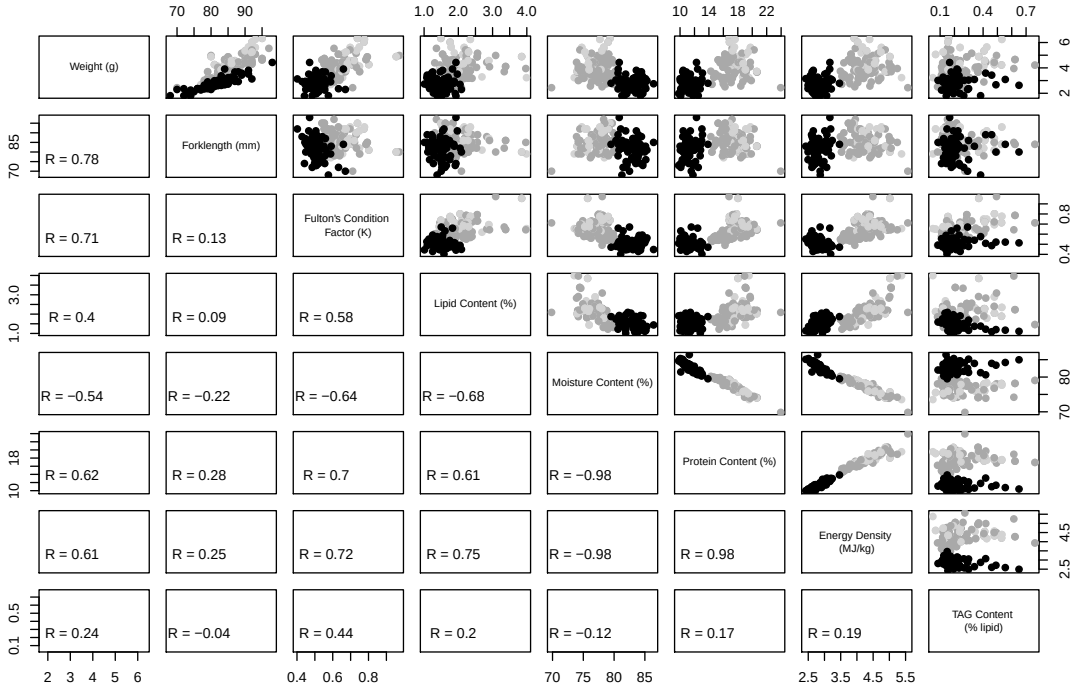

Figure 4.10: Correlation of condition metrics. Black points are for those that died during the experiment, dark grey for those that could not finish the swim trial, and light grey for those that finished the swim trial.

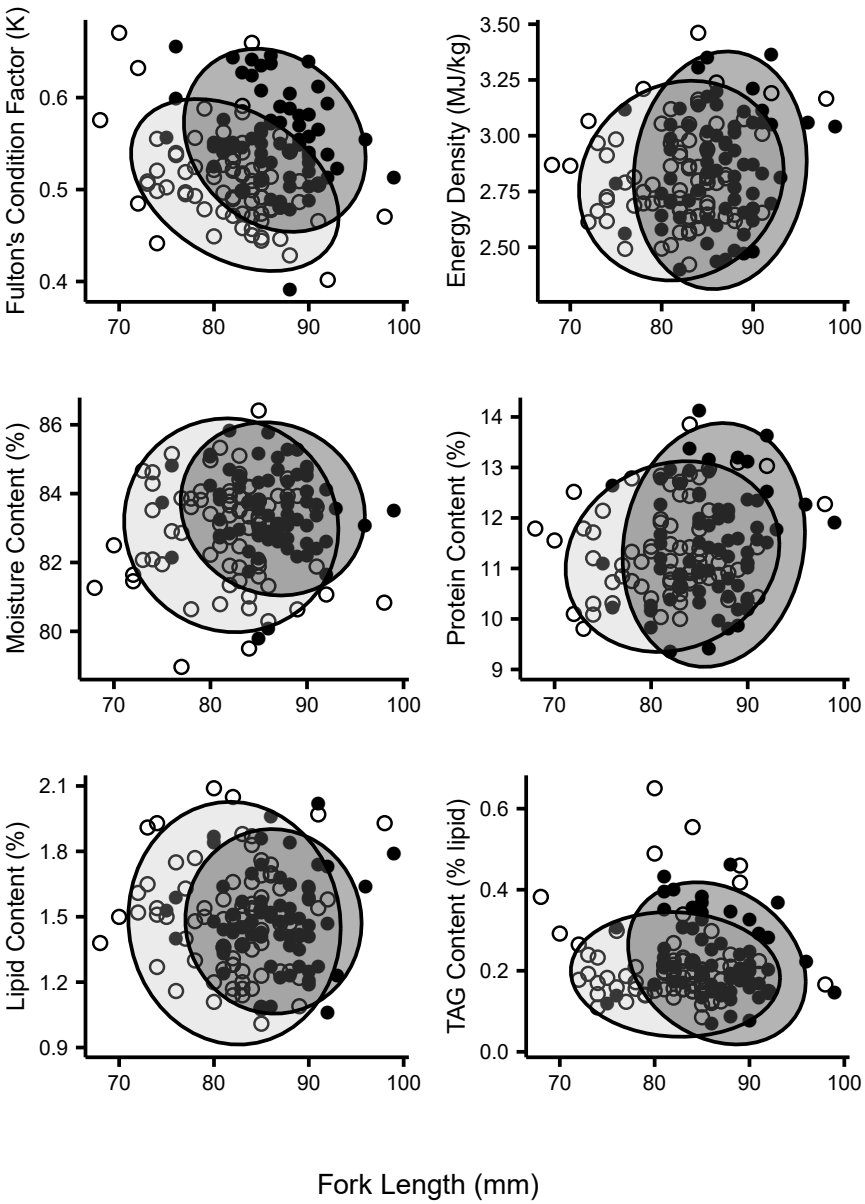

Figure 4.11: Size compared to condition variables for individuals that survived (closed circles) and individuals that died (open circles) during holding period. Oval region represents 95% confidence region.

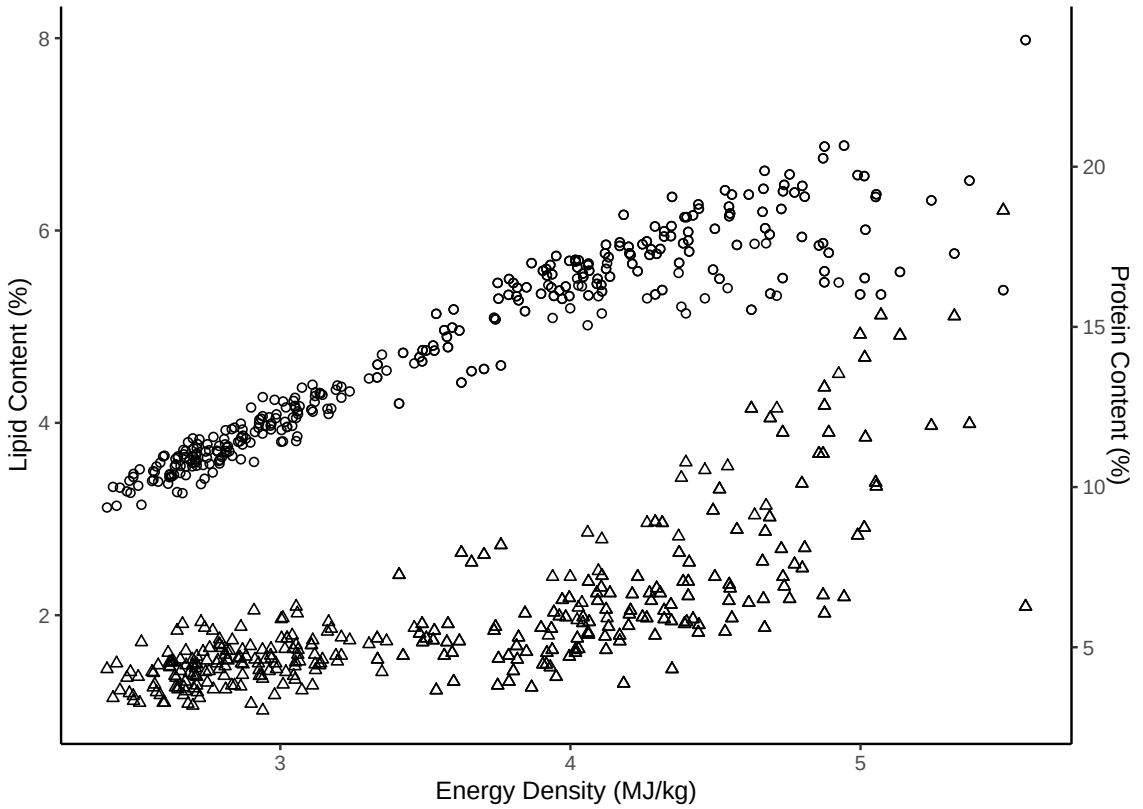

Figure 4.12: Changes in lipid and protein content contributions to energy density. Triangles represent lipid values, while circles represent protein values.

Chapter 5

Intra- and inter-population variation in sensitivity of migratory fish to changing marine prey phenology

5.1 Abstract

Predicting if and how species will respond to climate change impacts, such as phenological mismatches, is an important step for proactive conservation efforts. Global climate change is shifting the timing of life history events, which can result in phenological mismatches between predators and prey that impact the fitness or survival of the predators. If certain predator traits influence sensitivity to phenological mismatch, then understanding variation in these traits across or within populations may be helpful in predicting if and how a predator population will respond to mismatches. Pacific salmon (*Oncorhynchus* spp.) smolts can undertake challenging and energetically costly migrations from freshwater to marine environments, which, if mistimed, could lead to phenological mismatches with marine prey that may influence survival. Here we quantify intra- and inter-population variation in traits of sockeye salmon (*O. nerka*) smolts that influence sensitivity to starvation associated with phenological mismatch. We asked: what is the magnitude of intra- and inter-population variation in physical and energetic condition at different stages of emigration? and how would this trait variation influence survival during periods of starvation? We collected 259 sockeye salmon smolts from three populations at the initiation of the downstream riverine

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migration, and 212 smolts in the estuary after the riverine migration from eight populations within Skeena River Watershed, British Columbia. Measured traits such as fork length, weight, Fulton's condition factor, energy density, and lipid, protein, and moisture content, varied within and between populations, before and after migration. We estimated individual- and population-level starvation resistance using a previously developed model that predicts swim performance (a proxy for survival) from condition factor (estimated here using fork length at capture and predicted weight from the Wisconsin Bioenergetics Model). Starvation resistance, that is the number of days until predicted 'death', varied between 18 to 33 days for each population, and varied substantially within each population ranging as low as six days. These results reveal substantial within and across population sensitivity to starvation associated with phenological mismatch. Thus, freshwater ecosystem dynamics that influence smolt condition can carry over to influence sensitivity to phenological mismatch and potentially survival in marine environments.

5.2 Introduction

Global climate change is shifting the phenology of species at different rates, changing how and when species interact, potentially decoupling species interactions (e.g., predator-prey, parasite-host; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006; Thackeray et al. 2010). While some phenological mismatches may have survival or fitness consequences, not all phenological mismatches with food resources result in changes in survival (Durant et al., 2005; Pearce-Higgins et al., 2009; Ozgul et al., 2010). For example, predator-prey phenological mismatches between hatching of great tits (*Parus major*) and peak caterpillar abundance have led to a decrease in great tit fledgling survival (Visser et al., 2006). Alternatively, phenological mismatches between Soay sheep (*Ovies aries*) and peak spring vegetation did not influence lamb survival, possibly because lactating mothers could offset the energetic deficit using endogenous energy stored from previous seasons (Durant et al., 2005; Kerby and Post, 2013; Paoli et al., 2020). Thus, certain traits, such as energy stores or body condition, may influence if and how survival/fitness is affected by food limitation resulting from a phenological mismatch (i.e., the length of time until starvation), and therefore influence how sensitive that population or species is to a phenological mismatch. However, empirical evidence of differential sensitivity to phenological mismatch is sparse (Miller-Rushing et al., 2010; Thackeray et al., 2016).

Sensitivity to phenological mismatches is likely influenced by species-, population-, and individual-level traits (Cushing, 1990; Miller-Rushing et al., 2010). For example, species that have a single seasonal life-history event (e.g., univoltine organisms that reproduce once annually; Knell and Thackeray 2016), have simplified population structure (age or size-at-age; Ohlberger et al. 2014), rely heavily on a single prey type (specialist predators; Tucker et al. 2019), or are less plastic (both in regards to phenology, as well as prey type), are

more likely to be sensitive to phenological mismatches (Cushing, 1990; Durant et al., 2007; Miller-Rushing et al., 2010). However, the population- and individual-traits that may influence sensitivity to phenological mismatch have received much less attention. For example, perhaps different individuals or populations have traits (e.g., body size or energy stores) that render them more or less sensitive to the potential consequences of phenological mismatch. A clearer understanding of how intra- and inter-population variation in traits can mediate sensitivity to phenological mismatch could help predict vulnerability to climate-driven changes in phenology.

Pacific salmon (*Oncorhynchus* spp.) are renowned for their population-specific traits associated with local adaptation to variation in their energetically demanding migrations (Eliason et al., 2011) making them a model animal to examine how different population- and individual-level traits may influence sensitivity to phenological mismatch. Juvenile salmon rear in freshwater lakes and streams for up to several years before completing an energetically expensive non-feeding freshwater migration that can extend over hundreds of kilometers and take up to several weeks to complete. They then spend up to several months in the estuary before transitioning to the open ocean feeding grounds (Pearcy, 1992; Preikshot et al., 2012; Moore et al., 2016). Parts of the early marine migration may also be food limited. For example, juvenile salmon from the Fraser River and Salish Sea pass through the prey-scarce Johnstone Strait region prior to reaching the more prey-abundant open coastal waters (McKinnell et al., 2014; James, 2019). Survival during this early marine period has been linked to size and growth (Ward et al., 1989; Henderson and Cass, 1991; Beamish and Mahnken, 2001). Phenological asynchrony between juvenile outmigration and prey availability can lead to a decrease in individual and cohort survival of Pacific salmon (Ryding and Skalski, 1999; Chittenden et al., 2010; Satterthwaite et al., 2014; Malick et al., 2015a), but this is not universally the case (Scheuerell et al., 2009; Irvine and Akenhead, 2013; Evans et al., 2014; Gosselin et al., 2018). It is not clear why some species, populations, or individual salmon are more sensitive to phenological mismatches than others.

Carryover effects from freshwater rearing could influence the sensitivity of individuals and populations of Pacific salmon to challenging early marine rearing conditions associated with phenological mismatch. Juvenile salmon exhibit high intra- and inter-population variability in traits (e.g., size, condition factor, migration timing) which likely depend on factors such as density dependence, habitat productivity, and environmental conditions of freshwater rearing habitat (Beacham et al., 2014a; Freshwater et al., 2017; Carr-Harris et al., 2018; Jones et al., 2020). These differences may become important because juvenile salmon fuel their downstream migration predominately on endogenous energy reserves. Indeed, experimental evidence demonstrates that juvenile salmon with better body condition are more likely to survive long periods of starvation (Ferguson et al., 2010; Persson et al., 2018). Therefore, individuals and populations with higher body condition may be more likely to survive (i.e., less sensitive) periods of poor estuary or marine growth, conditions associated

with mismatch (Saloniemi et al. 2004; Fig. 5.1). Accordingly, individuals or populations of salmon of better body condition may be more robust to poor ocean conditions (Fig. 5.1).

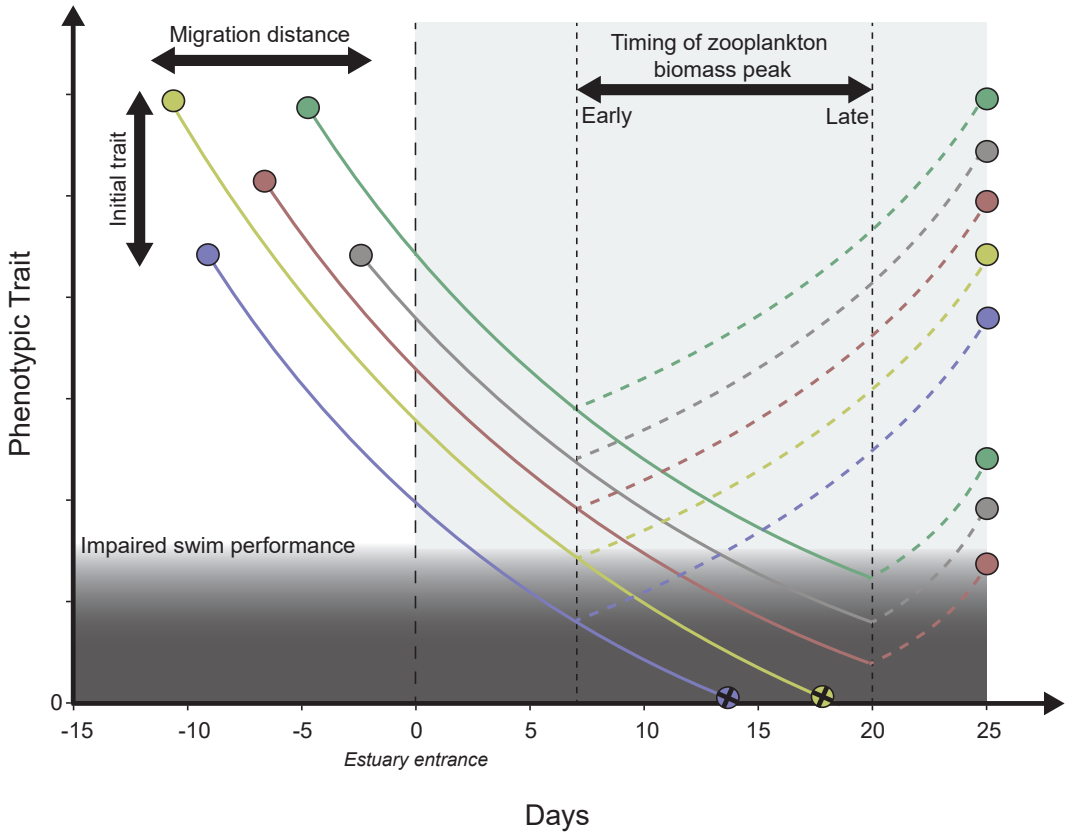

Figure 5.1: Conceptual figure describing how a phenotypic trait (such as condition factor) could impact sensitivity of different populations to a phenological mismatch. Five populations originate in freshwater and exhibit variation in body condition and migration length. As fish begin the non-feeding freshwater migration, body condition decreases until zooplankton biomass peaks. If the zooplankton abundance peak occurs close to the time of estuary entrance, all populations persist (phenological match). However, if peak zooplankton abundance is shifted to long after estuary entrance (phenological mismatch), populations of lower body condition (purple, then yellow, etc. . .) cannot persist. Thus, body condition could determine sensitivity to starvation associated with a phenological mismatch. When the interaction with ocean arrival and zooplankton phenology (exposure) is also considered, sensitivity and exposure show population-specific vulnerability to phenological mismatch.

Here we examine how variation in individual- and population-specific traits can influence individual- and population-level sensitivity to starvation associated with phenological mismatch. Specifically, we asked the questions: 1) what is the magnitude of intra- and inter-population variation in physical and energetic condition at different stages of emigration? and 2) how would these differences influence survival during periods of starvation (i.e., con-

ditions associated with/or exacerbated by a phenological mismatch)? Using wild sockeye salmon (*O. nerka*) smolts from three populations captured at the initiation of downstream migration at lake outlets, and from eight populations captured in the Skeena River estuary after freshwater migration, we compared physical and energetic condition within and across populations. We hypothesized that different rearing lakes and freshwater migration durations would produce smolts with differing body condition both across populations, but also that there would be substantial within population variation (MacDonald et al., 2019). We explored how this variation could translate into sensitivity to phenological mismatch using a bioenergetics model and a previously-developed model linking prolonged swim performance, a proxy for survival, with condition factor. We expected that variation in starvation resistance would be higher across populations than within populations based on differences in population-specific condition/size, estuary arrival timing, and migration duration, which could mean that populations of sockeye salmon will be differently impacted by phenological mismatch (Fig. 5.1).

5.3 Methods

The Skeena River drains approximately 55,000 km^2 of northwestern British Columbia and hosts the second largest sockeye salmon run in Canada. There are >30 genetically distinct Skeena River sockeye salmon populations; the majority of sockeye salmon (>90% in some years) are produced from Babine and Nilkitkwa Lakes, a linked series of the largest lakes in the Skeena River basin (Gottesfeld and Rabnett, 2008).

Juvenile Skeena River sockeye salmon rear for 1 – 2 years in natal lakes and rivers before they migrate to the Skeena River estuary in the spring. Lakes in the Skeena River basin range in primary productivity, size, and elevation, producing smolts across a range of sizes and conditions (Groot and Margolis, 1991; Gottesfeld and Rabnett, 2008). Depending on the population, smolts may migrate over 500 km before reaching the estuary, and typically arrive in the estuary in an ordered sequence based on migration distance and rearing location elevation (Carr-Harris et al., 2018). Population-specific smolt outmigrations are relatively pulsed, typically occurring over ~2 – 3 weeks; however, due to the staggered nature of their arrival, sockeye salmon smolts are continuously arriving to the estuary over an 8 – 10 week period starting in early May and ending in mid-July (Carr-Harris et al., 2018). The Skeena River estuary is ~1500 km^2, extending 75 km upstream of Port Edward to 50 km southwest through Ogden Channel and over 85 km Northwest through Chatham Sound at peak river discharge (Fig. 5.2). Skeena River sockeye salmon smolts spend between 2 – 18 days in the estuary before moving on to more northern coastal feeding grounds (Moore et al., 2016).

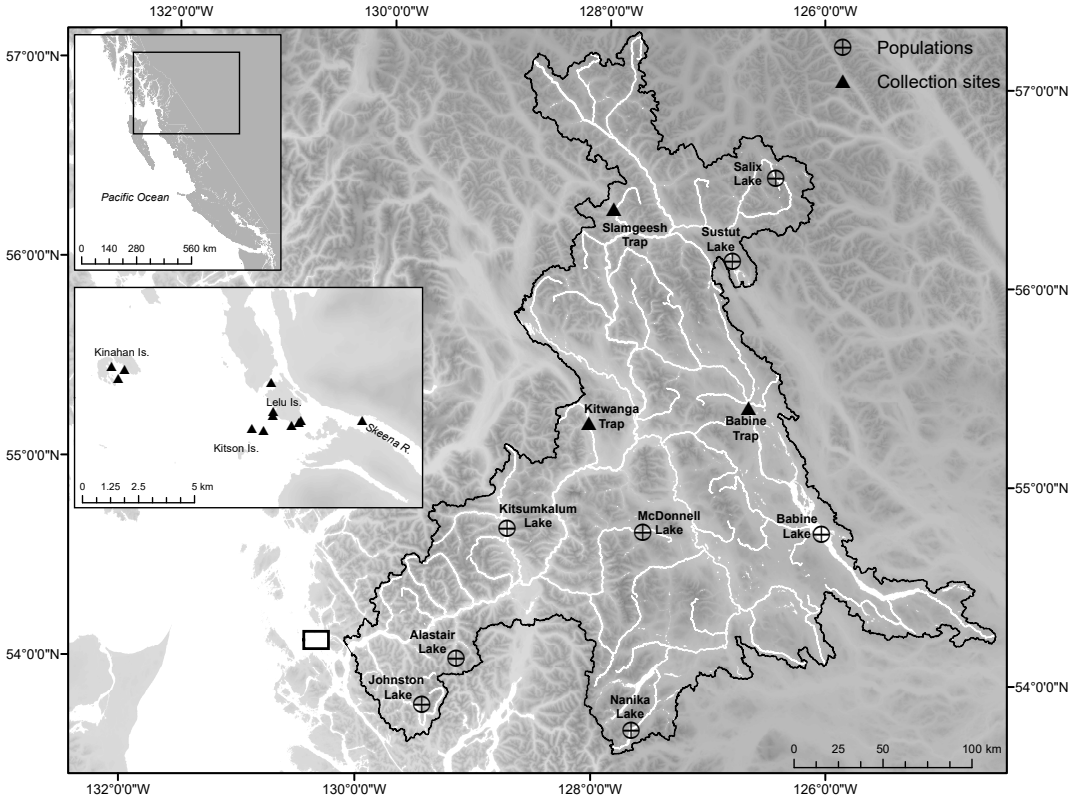

Figure 5.2: Map of the Skeena River with fence sites and estuary capture locations (inset). Black triangles indicate collection locations. Originating locations of populations captured in the Skeena River estuary after freshwater migration are denoted by circles with crosses through them.

5.3.1 Collection

Sockeye salmon smolts were collected from three freshwater lakes upon lake exit, as well as in the Skeena River estuary (Fig. 5.2). Sockeye salmon smolts were collected from Babine Lake every third day between May 4th and June 8th, 2015 (n = 85), and April 30th and June 9th, 2016 (n =103) using the Babine Lake smolt enumeration facility located at the Nilkitkwa Lake outlet (see Tiley et al. 2017 for more details on collection). Smolts were collected every other day from the outlet of Kitwanga Lake between April 21st and May 11th, 2016 (n = 36) and from Slamgeesh Lake outlet between April 26th and May 5th, 2016 (n = 35) using permanent full fence weirs. Sockeye salmon smolts were captured between May 5th and June 8th, 2015 (n = 77) and May 13th and June 21st, 2016 (n = 165) in the estuary as part of the North Coast Juvenile Salmon Monitoring Program (see Carr-Harris et al. 2018; Sharpe et al. 2019 for methodological details). Briefly, juvenile salmon were captured weekly using a purse seine (9.1 m deep, 73.2 m long, 51 mm mesh at tow end, 13 mm mesh at the bunt) towed for 5 min per set at 25 sites. A subset of sockeye salmon were

collected, and a fin clip was taken for genetic stock identification and stored in 95% ethanol until analyses (Beacham et al., 2005). Seven of the sockeye salmon smolts that were caught had external tags from Babine Lake. No genetic analyses were completed for these seven fish and they were assigned to Babine Lake. All fish were randomly selected, euthanized in an overdose of tricaine methanesulfonate (MS-222), and frozen at -20°C, for approximately one month, then transferred on dry ice to where they were stored at -80°C until analysis. All fish handling and sampling was performed in accordance with the animal care protocol (1158B-11) from the University Animal Care Committee at Simon Fraser University.

Genetic analyses were completed using microsatellite DNA analysis at Fisheries and Oceans Canada's Molecular Genetics Laboratory (Pacific Biological Station, Nanaimo, British Columbia; Beacham et al. 2005). Each fish was assigned to a population probabilistically using allele frequencies from known samples collected from 20 regions throughout the Pacific Northwest (Beacham et al., 2014a). Only fish with a percent certainty greater than 75% were included in this analysis. There are multiple spawning sites within the Babine Lake system but they are difficult to genetically isolate and generally have less than 75% certainty, so all populations assigned from Babine and Nilkitkwa Lakes were assigned to a generic Babine Lake population (Beacham et al., 2014b). These populations almost all rear in Babine Lake, and so share rearing conditions. Of the 242 samples run for DNA, 24 had less than 75% certainty in population assignment and were removed from analysis, and seven did not have enough DNA to test.

5.3.2 Condition determination

We determined the physical and energetic condition of fish by measuring fork length (FL), and wet weight (g) of thawed fish, as well as determining proximate body constituents (percent lipid, percent water, and percent ash). All fish captured in 2015 were run for proximate body condition analyses, however, we ran only a random subset of 81 of the 110 Babine Lake sockeye salmon smolts captured in the estuary in 2016. Fulton's condition factor (K) was determined by:

$$K = \frac{Wt}{FL^3} * 100 \tag{5.1}$$

where weight Wt is in grams and fork length FL is in centimeters.

Proximate body composition was determined using protocol outlined in Chapter 4 and Crossin and Hinch (2005) adapted from Bligh and Dyer (1959) and Higgs et al. (1979). Briefly, lipid percent was determined from a subsample of 0.3 ± 0.015 g of homogenate of whole fish which was mixed with methanol, chloroform, and water in ratio of 1:1:0.48, homogenized, and decanted. Upon formation of biphasic layers, the chloroform layer was removed, measured, and evaporated on pre-weighed aluminium dishes, leaving only lipid remaining, which could be weighed. Moisture content was determined by drying 0.3 ±

0.015 g of homogenate at 100°C for 16 – 20 h. Ash was determined by combusting the 0.3 ± 0.015 g of homogenate to 600°C in a muffle furnace for 2.5 hrs.

Percent whole body protein was determined from percent water (W), percent lipid (L), and percent ash (A) (Brett and Groves, 1979; Breck, 2008):

$$P = 100 - (W + L + A) \tag{5.2}$$

Energy density was determined from the amount of lipid per fish multiplied by the energy density of lipid (0.0362) added to the amount of protein multiplied by the energy density of protein (0.0201) (Brett and Groves, 1979).

5.3.3 Bioenergetic modeling

To estimate the change in fish condition through time, we used a modified version of the Wisconsin Bioenergetics Model parameterized for juvenile rainbow trout (*O. mykiss*; Tyler and Bolduc 2008; Deslauriers et al. 2017; Hanson et al. 1997). We fit the model with 0 g consumption to simulate starvation conditions and used initial fish weight and regional water temperatures (corresponding to regions of the Skeena River system experienced during downstream migration) to model weight change over 45 days of migration (see Section 5.7 Supplemental Materials). Bioenergetics simulations were started in similar temperature conditions in which fish were captured. For example, fish captured at the Babine Lake trap, were modelled as experiencing Babine River temperatures for nine days, and mainstem conditions for four days, reflecting current estimates of migration timing (C. Carr-Harris Pers. Comm.). After the 13-day freshwater migration, fish were modelled with estuary water temperatures. Fish captured in the estuary were modelled with only estuary water temperatures – see Section 5.3.3.1 Water Temperature for water temperature migration profile for each capture site (Fig. 5.6).

Using the estimated daily weight from the Wisconsin Bioenergetics Model, we calculated the change in condition factor using initial fork length (Equation 5.1). This produced a daily estimate of condition factor which decreased throughout the 45-day period.

This modeling depends on a variety of assumptions: 1) metabolic processes use the same amount of energy in freshwater compared to saltwater. It is possible that energy use in saltwater is higher due to increased osmoregulatory requirements, however this has not been robustly quantified for juvenile salmon (Wagner et al., 2006). The Wisconsin Bioenergetics Model does not have parameters for salmon in the ocean, so we used the data available, and recognize that estimated energy use in the ocean is likely conservative. 2) Metabolic rate remains the same for starving and fed fish. This is also likely a conservative estimate, as starving fish have decreased activity and likely have decreased metabolic rate. Again, these parameters are not available. However, in Chapter 4 sockeye salmon were held without food

for 61 days and weight was measured weekly. We compared the observed change in weight of those fish to predicted change in weight using the Wisconsin Bioenergetics Model, and found the results were similar for the first three weeks (Fig. 5.7). Therefore, model estimates did correspond to observed patterns, but it should be noted that bioenergetics models make assumptions and are a simple way to explore energy use.

5.3.3.1 Water temperature

Water temperature migration profiles were created for each capture site based on the most likely migration timing and available temperature stations in the Skeena River and Skeena River estuary. For the Skeena River estuary, we used mean daily temperature between May 15th and June 30th, averaged across years 1990 – 2019, from station 46145 - Dixon Entrance, (54.370°N; 132.44°W). We relied on two government stations for creating freshwater temperature migration profiles (https://wateroffice.ec.gc.ca/); data from station 08EB005 (55.717°N; 127.687°W) above Babine River confluence and station 08EB003 (55.301°N; 127.673°W) below Babine River confluence. For temperatures from the Babine River, we used mean daily temperature averaged across sites for 2016 and 2017 which were collected from 15 stations along the Babine River (K. Pitman, Pers. Comm.). For fish captured at the Babine Fence, we modelled temperature based on a nine-day migration through the Babine River (May 9th – 17th; using daily averaged Babine River temperature for 2016/17), and four-day migration (May 18th – 21st) through the Skeena mainstem (station 08EB003), for the remaining 32 days we used Skeena River estuary water temperature data (May 22nd – June 22nd; station 46145). For fish captured at the Slamgeesh fence, we used water temperatures from station 08EB005 above the Babine River confluence for nine days (May 9th – 17th), water temperatures from station 08EB003 below the Babine River confluence for four days (May 18th – 21st) and the remaining days used data from the Skeena River estuary (May 22nd – June 22nd; station 46145). Finally, the Kitwanga population is closer to the Skeena River estuary with likely a much shorter migration time. Therefore, we used water temperatures from the Skeena River below Babine River confluence for seven days (May 18th – 24th; station 08EB003) and used estuary water temperature profile for the remaining 38 days (May 25th – July 1st; station 46145; Fig. 5.6).

5.3.4 Predictive modeling

We used a previously developed model of swim performance and smolt condition to predict whether a smolt would complete or fail a prolonged swim performance test based on its condition factor (for details see Chapter 4). Prolonged swim performance affects migratory capacity, as well as the ability of fish to capture prey, and evade predators, and thus is linked to survival and fitness (Plaut, 2001). Briefly, sockeye salmon smolts were captured from Chilko Lake, and transported to a holding facility where they were held without food. Seven days after capture, fish were transferred from freshwater to fully saline (28 – 30 ppt)

water over a 36-hr period. Every week for six weeks 18 fish underwent a prolonged swim performance challenge. Nine fish were placed in a swim tunnel (9 cm wide, 15 cm tall, 142 cm long), and held for 12 min at a flow rate of ~0.085 m/s (~1 BL/s), over a period of 12 min flow was slowly increased to 0.50 m/s (~4.5 – 6.4 BL/s), and remained at that flow rate for 90 min, or until the fish could no longer swim. Fish failed the swim test if they did not complete the 90 min swim, and fish that completed the 90 min swim test passed. Fish were euthanized with an overdose of MS-222 (0.5 g/L), fork length was measured (FL; mm), and fish were weighed (g), frozen on dry ice, and stored at -80°C. Proximate body composition was determined using the methods of described in Section 5.3.2 Condition Determination.

We used a generalised linear model with a binomial distribution and logit link function to create models from combinations of standardized and centered independent smolt condition variables to predict the probability of a fish completing the 90 min prolonged swim test. The most parsimonious model (defined by Akaike Information Criterion corrected for small sample sizes (AIC_c)) included only condition factor. We used k-fold validation to determine accuracy of the model, whereby the model was re-parameterized with 90% of the data (training dataset) and used to predict remaining 10% of data (test dataset). To be more conservative, we ran the model with predicted probabilities of ≥ 0.3 = passed and <0.3 = failed, and these predictions were compared to observations to determine model predictive performance. This procedure was repeated 1000 times with samples randomly assigned to either training or test datasets. We found that the generalised linear model using condition factor as the predictor variable could correctly predict whether a fish could complete the swim trial 78.7% of the time.

$$logit(\phi) = 1.679 * CF - 1.620 \tag{5.3}$$

where ϕ is the binary swim performance outcome (pass/fail), and CF is Fulton's condition factor.

We used this generalised linear model (Equation 5.3) to predict whether a wild-caught fish could complete the swim performance trial, where failure to complete the swim performance trial was a proxy for death (see Chapter 4). Using the predicted daily weight from the Wisconsin Bioenergetics Model for each of the temperature scenarios, and assuming the fork length would not change over a period of starvation, we calculated daily condition factor for each fish captured in the estuary or at the freshwater fences, and each water temperature scenario (Fig. 5.8). We used the predicted daily condition factor to estimate daily probabilities of completing the swim performance test. As fish had 0 g consumption (unfed), these daily probabilities slowly decreased as condition factor decreased until probability was less than 30% that fish could complete the swim performance test. We then determined starva-

tion resistance; the number of days between capture and the first day that the probability of a fish completing the swim performance test fell below the 30% threshold (Fig. 5.4).

5.3.5 Statistical analyses

We compared population means of each physical and energetic condition metric (fork length, weight, Fulton's condition factor, energy density, and protein, moisture, and lipid content) for three populations captured before riverine migration and the eight populations captured in the estuary, separately. Data were tested for normality and homoscedasticity. We compared population means using ANOVAs. If the parameter estimates from the ANOVA were significantly different, we used post-hoc pairwise Bonferroni t-tests to identify significantly different populations. We applied an adjusted α value of 0.00625 based on Bonferroni correction for 8 tests, in order to minimize the increased false positive error rates associated with multiple statistical tests (Field et al., 2012).

To quantify within and across population variation, we compared variance that was explained by all populations vs. total residual variance. To accomplish this, we ran an intercept-only random effects model with a single physical or energetic metric as the dependent variable and population as a random effect. We calculated the percent of the variance absorbed by the population random intercept relative to the total variation (variance of the population intercept divided by the sum of the population intercept and individual residual variance estimate, multiplied by 100). A value close to 100 suggests that among-population variation explains most of the total variation, such that two individuals from the same population are likely to be more similar that two individuals from different populations. A value near zero suggests that the among-population variation is relatively low, such that two individuals from different populations are equally likely to be similar as two individuals from the same population.

All statistics were performed in R statistical computing environment (v 3.6.3; R Core Team 2020) using RStudio GUI (v 1.2.5033, 2019) and the following packages: `AICcmodavg` (Mazerolle, 2017), `lme4`(Bates et al., 2015) and `ggplot2` for graphing (Wickham, 2009). The Fish Bioenergetics 4.0 GUI was used with R statistical computing environment for the Wisconsin Bioenergetics Model simulations (Deslauriers et al., 2017).

5.4 Results

5.4.1 Variation in freshwater captured populations

Physical and energetic condition metrics varied widely both across individuals within a population and between populations captured in freshwater. For example, smolts captured at the Babine Lake outlet had highly variable fork lengths (mean 79.1 mm, range 65 – 98 mm, SE $\pm$ 0.5; n = 188), that differed from smolts captured at Slamgeesh (mean FL 99.9 mm, range 80 – 124 mm, SE $\pm$ 1.4; n = 35) and Kitwanga lakes (mean FL 107.3, range 97 –

Table 5.1: Physical and energetic condition of sockeye salmon smolts collected at freshwater lake exit at three smolt fences and at regions in the Skeena River estuary.

	Freshwater Fences			Populations captured in the Skeena River estuary[2]							
	Babine Lake	Slamgeesh Lake	Kitwanga Lake	Johnston Lake	Alastair Lake	Kalum Lake	McDonnell Lake	Babine Lake	Nanika Lake	Sustut Lake	Salix Lake
Sample Size	188	35	36	3	5	13	2	130	5	13	10
Median Percent Stomach Fullness[2]	0	0	0	NA	100	100	NA	75	NA	100	100
Fork Length (mm)	79.1	99.9	107.4	57.3	76.4	67.1	74.0	77.7	74.6	76.5	92.3
(SE)	±0.5	±1.4	±1.0	±3.8	±4.4	±2.2	±2.0	±0.6	±4.1	±1.6	±2.4
Weight (g)	4.67	9.47	14.06	1.83	4.68	3.37	3.59	4.59	4.38	4.77	8.54
(SE)	±0.08	±0.46	±0.39	±0.43	±0.82	±0.31	±0.32	±0.10	±0.50	±0.27	±0.61
Fulton's Condition Factor	0.94	0.93	1.13	0.94	1.01	1.09	0.88	0.96	1.06	1.06	1.07
(SE)	±0.01	±0.01	±0.01	±0.05	±0.03	±0.04	±0.01	±0.01	±0.08	±0.04	±0.03
Energy Density (MJ/kg)	4.43	5.07	6.15	4.22	4.46	4.24	4.31	4.30	4.53	4.77	5.02
(SE)	±0.04	±0.08	±0.08	±0.18	±0.01	±0.09	±0.10	±0.03	±0.14	±0.13	±0.09
Water(% wet weight)	78.46	76.12	73.03	78.17	77.17	78.06	77.84	78.24	76.96	76.46	75.95
(SE)	±0.11	±0.05	±0.25	±0.81	±0.61	±0.42	±0.51	±0.09	±0.46	±0.41	±0.31
Protein (% wet weight)	15.87	17.61	17.98	16.85	17.68	17.14	17.24	16.47	17.36	17.62	17.84
(SE)	±0.05	±0.26	±0.13	±0.65	±0.44	±0.38	±0.31	±0.06	±0.32	±0.18	±0.25
Lipid (% wet weight)	3.42	4.22	7.00	2.31	2.51	2.20	2.33	2.74	2.87	3.41	3.96
(SE)	±0.10	±0.16	±0.20	±0.17	±0.20	±0.12	±0.12	±0.07	±0.32	±0.31	±0.18
Starvation Resistance (days)	25	26	33	20	25	27	18	22	27	27	29
(Range)	(6 – 44)	(14 – 33)	(27 – 38)	(15 – 23)	(21 – 30)	(19 – 38)	(17 – 18)	(7 – 38)	(13 – 35)	(9 – 36)	(23 – 35)

[1] Pairwise comparisons of populations captured in the estuary are shown in the supplemental methods.
[2] Stomach contents analyzed for 2016 samples only.

120 mm, SE ± 1.0; n = 36; Table 5.1). Variation among populations was higher than within populations (percent of variability explained by population was >60%) for all metrics of physical and energetic condition for salmon captured at the three freshwater fences prior to riverine migration; Table 5.2).

Table 5.2: Percent of the total variability in physical and energetic condition explained by populations captured in freshwater and in the Skeena River estuary.

	Freshwater Captured Populations	Estuary Captured Populations
Sample Size of Individuals (Populations)	259 (3)	181 (8)
Fork Length (mm)	83.3%	64.6%
Weight (g)	89.7%	70.2%
Fulton's Condition Factor	61.0%	19.4%
Energy Density (MJ/kg)	75.4%	39.1%
Water (% wet weight)	75.9%	33.4%
Protein (% wet weight)	61.7%	25.9%
Lipid (% wet weight)	68.1%	32.9%
Starvation Resistance	43.3%	19.4%

Mean energetic and physical condition metrics differed significantly among populations for smolts captured at each fence site (fork length (F value = 374.1, df = 2, p<0.0001), weight (F value = 590.4, df = 2, p<0.0001), lipid content (F value = 119.1, df = 2, p<0.0001), water content (F value = 203.4, df = 2, p<0.0001), protein content (F value = 123.5, df=2, p<0.0001), Fulton's condition factor (F value = 72.1, df = 2, p<0.0001), and energy density (F value = 190.4, df = 2, p<0.0001)). Post hoc pairwise Bonferroni t-tests demonstrated that all three populations significantly differed from each other, with fork length (p<0.0001), weight (p<0.0001), and energy density (p<0.0001) all higher in Kitwanga Lake smolts, followed by Slamgeesh Lake smolts, and Babine Lake smolts having the lowest condition metrics (Table 5.1). Water content was also significantly different among groups (p<0.0001), but as expected, displayed the opposite trend with Babine Lake smolts having the highest water content, followed by Slamgeesh Lake smolts, and Kitwanga Lake smolts (Table 5.1). Mean protein content differed significantly between Babine Lake and Kitwanga Lake smolts (p<0.0001), and Babine Lake and Slamgeesh Lake smolts (p<0.0001) but did not differ between Slamgeesh Lake and Kitwanga Lake smolts (p=0.25). Protein content was higher in Kitwanga and Slamgeesh Lakes compared to Babine Lake smolts. Both Fulton's condition factor and mean lipid content differed significantly between Babine Lake and Kitwanga Lake smolts (p<0.0001), and Kitwanga Lake and Slamgeesh Lake smolts (p<0.0001), but not between Babine Lake and Slamgeesh Lake smolts (CF p=1, lipid p=0.0022; Fig. 5.3). Fulton's condition factor and lipid content was higher in Kitwanga Lake smolts compared to either Babine or Slamgeesh Lake smolts. Generally, smolts from Kitwanga Lake were larger, and had higher physical and energetic condition than smolts from Slamgeesh or

Babine Lakes, and Slamgeesh Lake smolts had higher condition metrics than Babine Lake smolts.

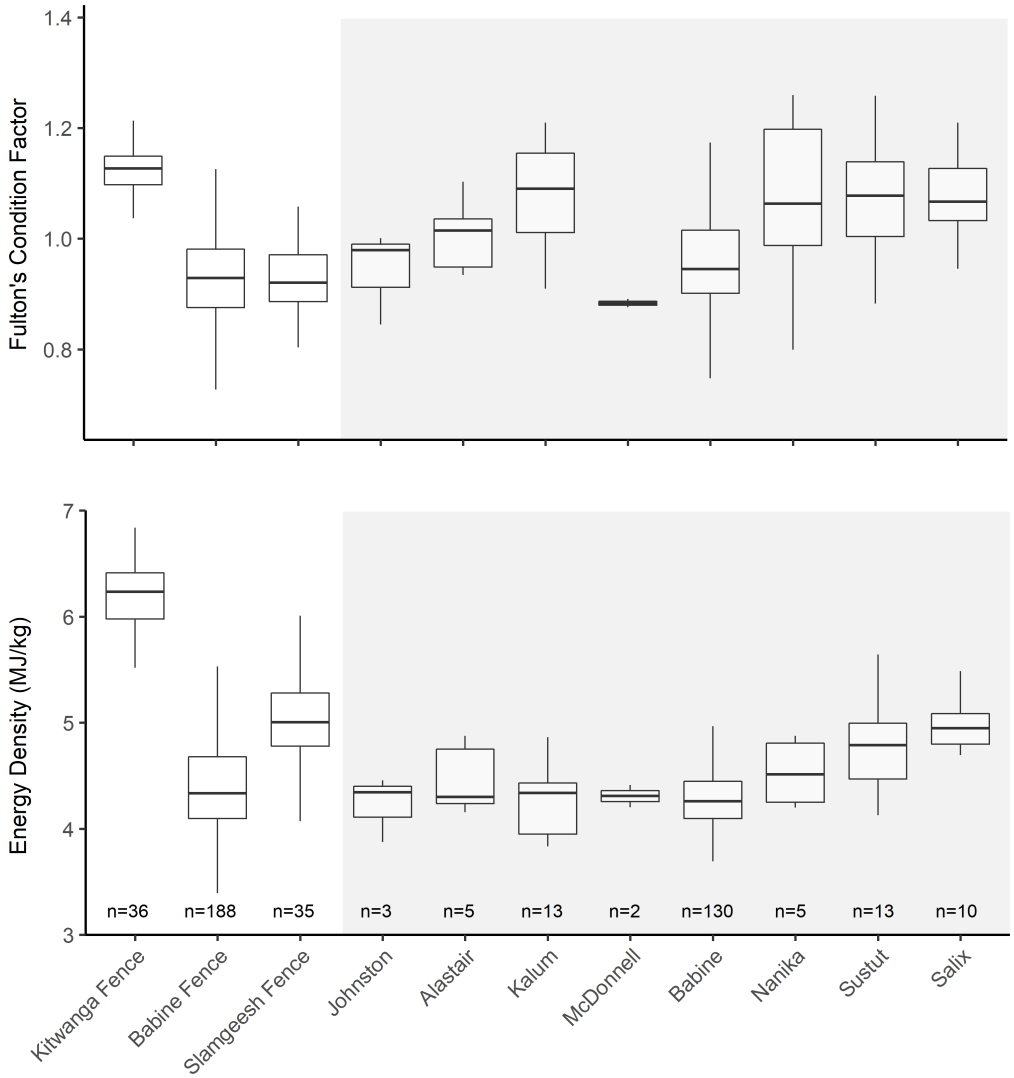

Figure 5.3: Fulton's condition factor (top) and energy density (bottom) of sockeye salmon smolts from three different populations captured from freshwater (white background) and eight different populations captured in the estuary (grey background). Boxplots show the 25^{th}, median, and 75^{th} percentiles.

5.4.2 Variation in estuary captured populations

Body condition metrics varied both within and across populations sampled in the estuary. For example, smolts ranged in Fulton's condition factor between 0.67 to 1.39 across populations (Table 5.1). Populations varied significantly in physical and energetic condition (fork

length (F value = 14.46, df = 7, p<0.0001), weight (F value = 19.59, df = 7, p<0.0001), lipid content (F value = 5.593, df = 7, p<0.0001), water content (F value = 9.492, df = 7, p<0.0001), protein content (F value = 9.6, df = 7, p<0.0001), Fulton's condition factor (F value = 5.286, df = 7, p<0.0001), and energy density (F value = 9.369, df = 7, p<0.0001; Table 5.1). Smolts from Johnston and Alastair Lakes were generally smaller and had the lowest condition metrics, compared to Sustut and Salix Lake smolts, which were much larger and of better condition (Fig. 5.3; see Tables 5.3 - 5.9 for pairwise comparisons). However, among-population variance was lower for estuary samples than among-population variance for freshwater sites, with the percent of variation explained by population being <40% for all physical and energetic condition metrics, with the exception of fork length and weight (Table 5.2).

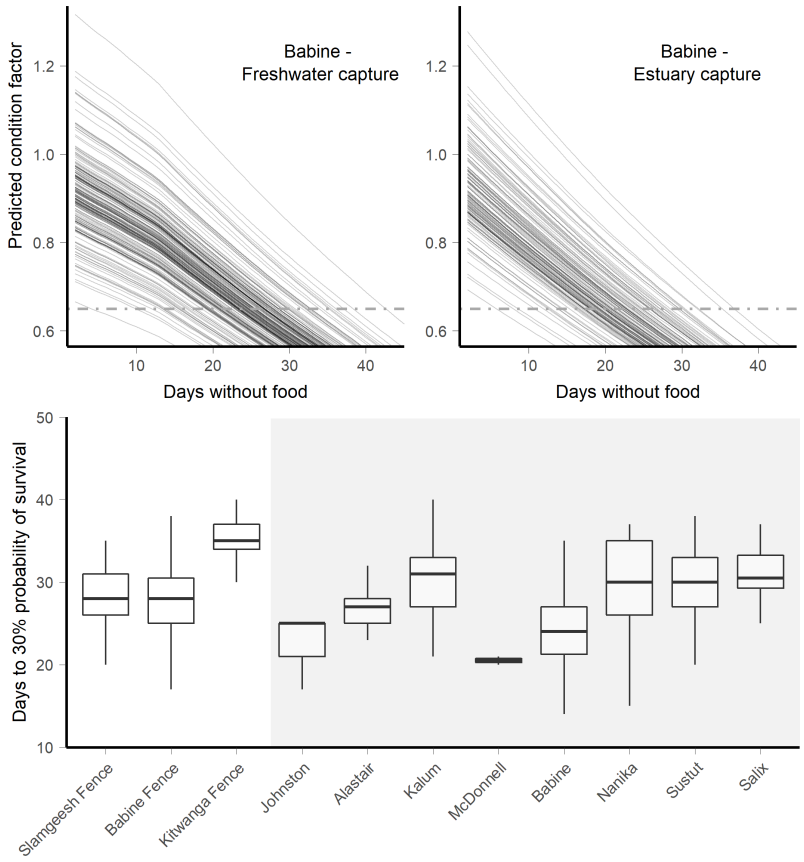

Figure 5.4: Top – Predictions of Fulton's condition factor based on predicted weights from Wisconsin Bioenergetics Model output for fish captured at fence sites (left) and in the estuary (right). The dashed line represents the critical value 0.65, when fish had 30% probability of completing the swim trial according to Equation 5.3. Bottom - Number of days to 30% probability of survival using swim performance model, for fish captured at fence sites or in the estuary. Grey shaded region represents estuary residence. Boxplots show the 25^{th}, median, and 75^{th} percentiles.

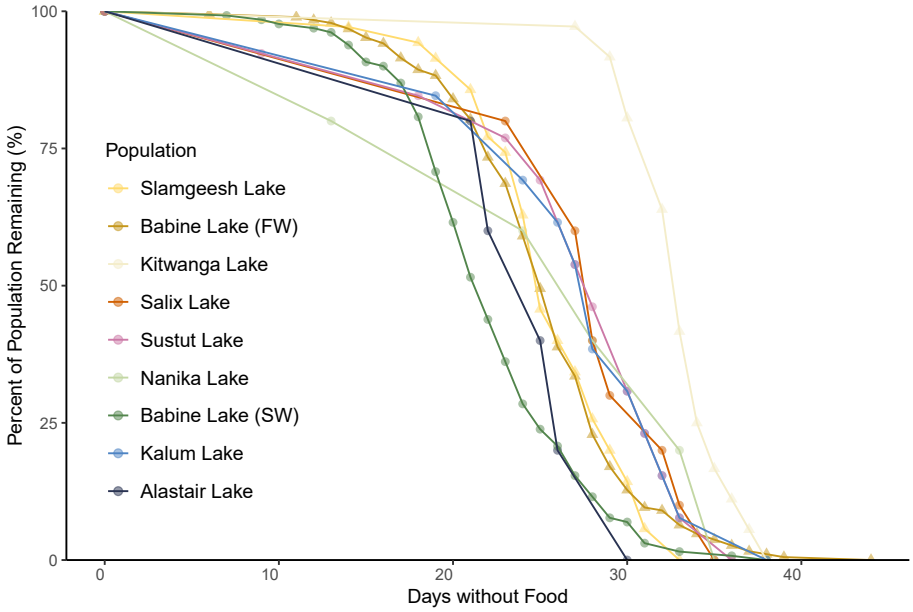

Figure 5.5: Percent of population remaining based on days to 30% survival probability using swim performance model and estimated Fulton's condition factor for each population. Triangles represent populations sampled in freshwater (FW), before freshwater migration, and circles represent populations sampled in the estuary (SW), after freshwater migration.

5.4.3 Variation in estimated starvation resistance

Populations had variable mean modelled starvation resistance. By integrating observed patterns in traits with previous experimental relationships between traits and swim performance (survival), we estimated that starvation resistance was significantly longer by ~3 days for smolts captured in fresh water (average = 26, range 6 – 44 days) versus those captured in the estuary (average = 23, range 7 – 38 days) (F value = 32.22, df = 1; $p<0.0001$). Populations captured at lake outlets also varied in mean predicted starvation resistance (F value = 97.52, df = 2, $p<0.0001$; Table 5.1), with Kitwanga Lake smolts having significantly longer predicted starvation resistance (33 days, range 25 – 43 days) compared to Slamgeesh (26 days, range 14 – 36 days; $p<0.0001$) or Babine (25 days, range 5 – 45 days; $p<0.0001$) Lake smolts. Similarly, populations captured in the estuary varied significantly in mean predicted starvation resistance (F value = 12.18, df = 7, $p<0.0001$), with the mean for most populations between 18 to 29 days, but with substantial intra-population variability (Table 5.1). Indeed, among-individual variability was higher in predicted starvation resistance such that population explained less variance in either freshwater or the marine environment (Table 5.2). Bonferroni post hoc pairwise comparisons demonstrate that starvation resistance varied significantly between Babine and Salix/Bear ($p<0.0001$), Sustut ($p<0.0001$), and Kalum ($p<0.0001$) Lake populations, between Kalum and McDonnell lake

smolts ($p<0.0001$), as well as between Salix/Bear and Johnston ($p<0.0001$) and McDonnell Lake ($p<0.0001$) populations (Table 5.10). In sum, starvation resistance varied based on migration stage (lake outlet/estuary) as well as within and across populations.

Populations across both sample locations varied somewhat in the modelled time it takes for 50% of population to die (Fig. 5.5). The days to 50% mortality of freshwater-captured populations from Babine and Slamgeesh Lakes was 25 days, and Kitwanga Lake was 33 days. Similarly, Kalum, Nanika, Salix/Bear and Sustut Lake populations captured in the estuary had 28 days to 50% mortality, while Alastair had 25 and Babine Lake population had 22 days to 50% mortality.

5.5 Discussion

Here we show that juvenile sockeye salmon exhibit a high degree of within and among population variation in traits related to body condition; this trait variability indicates differential sensitivity to food deprivation which can occur during phenological mismatches. Thus, body condition could be useful in estimating sensitivity and predicting vulnerability to future phenological shifts and mismatch. As climate change shifts the phenology of species, understanding which species and populations could be most vulnerable to changes in food availability associated with phenological mismatches is of increasing importance, especially for species of cultural or commercial importance (Cushing, 1990; Miller-Rushing et al., 2010; Thackeray et al., 2016).

Observed variation in Skeena River sockeye salmon body condition translates into substantial intra- and inter-population variation in sensitivity to poor feeding conditions, or timing of prey abundance relative to predator demand. For example, smolts sampled from the Babine Lake outlet have an average Fulton's condition factor of 0.94 (range = 0.68 – 1.34) corresponding to a starvation resistance of 25 days but ranging to as little as six days. Given that down-river migration of Babine Lake sockeye smolts is thought to be 7 – 12 days (C. Carr-Harris, Pers. Comm.), smolts at the low range of the condition factor likely do not survive even the freshwater migration. Smolts from the Slamgeesh Lake population had similar mean Fulton's condition factor and starvation resistance compared to smolts from Babine Lake population, but had fewer lower conditioned individuals, possibly a trait selected for due to the increased energy requirements of a longer freshwater migration. Indeed, the lowest Fulton's condition factor observed for Slamgeesh Lake smolts was 0.76 corresponding to a 14-day starvation resistance. In contrast, smolts from the Kitwanga Lake population had significantly higher Fulton's condition factor (mean = 1.13, range = 0.76 – 1.06) and increased starvation resistance (mean = 33 days, range = 27 – 38 days), despite a much shorter freshwater migration than either Babine or Slamgeesh Lake populations. Differences in freshwater growing and migrating conditions likely also influence the intra- and inter-population variability in condition, and thus sensitivity to phenological mismatch.

Trait variability of sockeye salmon captured in the estuary further demonstrates variability in sensitivity to phenological mismatch. Average Fulton's condition factor for fish captured in the estuary varied between 0.72 to 1.39 corresponding to a predicted average starvation resistance of 26 days which ranged to as low as seven days. Thus, smolts of low body condition may be particularly susceptible to a phenological mismatch that either reduces or delays the amount of prey (Saloniemi et al., 2004). Surprisingly, predicted starvation resistance for fish captured in the estuary was similar to fish captured before freshwater migration, even though the fish captured in freshwater had yet to complete a non-feeding freshwater migration that may last up to two weeks. While starvation resistance was statistically different between freshwater and estuary captured populations, the difference was only three days greater, which is likely not biologically significant given a freshwater migration of over a week. We anticipated that condition-selective mortality would occur during the migration (Rondorf et al., 1985; Tucker et al., 2016) and that migrating fish would use energy stores during the downstream journey, leading to lower intra-population variation of fish captured in the estuary compared to lake outlets. However, we observed the opposite trend. Within population variation was higher for fish captured in the estuary compared to those captured at lake outlets. The increase in intra-population variation was likely due to differences in feeding and migration behaviour, with some smolts beginning to feed in the estuary sooner than others, which may have masked observations of any possible effects of condition-selective survival in the riverine migration. In fact, many smolt stomachs were near-full despite capturing them at the river mouth, highlighting the importance of estuary habitats for energetic recovery of migrating salmon. Indeed, estuaries are important nursery grounds for some salmon species, providing enriched feeding and growing opportunities (Healey, 1982; Thorpe, 1994; Quinn, 2018; Seitz et al., 2020). This represents a rare example of a study that translates variability of traits into variability in sensitivity to phenological mismatch.

Freshwater conditions influence smolt body condition and thus could influence sensitivity to phenological mismatch, early marine survival, and climate change sensitivity (Reed et al., 2010). Alteration to the historic migration schedule (e.g., barriers such as dams) or changes to freshwater habitat (e.g., from decreased habitat availability/quality) that decrease fish condition at marine entry could negatively impact early marine survival. Similarly, increased competition (through stocking or natural variation in spawners) could result in decreased average body condition for smolts (Bjornn et al., 1968; Einum et al., 2006, 2011; Grossman and Simon, 2020), which could increase sensitivity to phenological mismatch. Reciprocally, if population densities decrease and relax competition, the potential increase in body condition could provide a mechanism supporting the high compensatory capacity and resilience of salmon (Healey, 2009). These effects may not be immediately evident, as phenological mismatches do not occur in every year. While freshwater carryover effects can present a chal-

lenge, they also mean that freshwater habitat improvements that improve smolt condition could potentially foster climate resilience.

Starvation resistance may not be entirely reflective of sensitivity. Starvation resistance and thus predicted survival is likely an underestimate given that predictions of weight loss were based on laboratory studies where fish would use less energy than in natural settings. Despite this conservative approach, these estimates show that smolts have only a few weeks of energy stores. Apart from starvation resistance, even a modest delay in marine growth could increase future predation risk (Beamish and Mahnken, 2001; Duffy and Beauchamp, 2011; Friedland et al., 2014). Therefore, starvation resistance is not necessarily indicative of mortality rates, which may be higher due delayed marine growth.

Understanding species and population sensitivity to mismatch is the first step to identifying vulnerability and predicting impacts of climate-driven phenological mismatch. Two factors work together to determine vulnerability: sensitivity and exposure (Williams et al., 2008). Here we have demonstrated within- and across- population differences in body condition which could influence sensitivity to phenological mismatch. Other traits in addition to body condition such as diversity of life history expression (e.g., life span, age-at-maturity), physiology (e.g., disease resistance, metabolic scope) and plasticity, could predict individual- or population-level sensitivity to phenological mismatch (Ohlberger et al., 2014; Knell and Thackeray, 2016; Tucker et al., 2019). For example, populations with complex age structure may be better able to buffer total or partial loss of a cohort due to mismatch (Ohlberger et al., 2014). Current phenotypic diversity and future climate warming could influence frequency of exposure of salmon smolts to phenological mismatch. For example, Carr-Harris et al. (2018) found that Skeena River sockeye salmon smolts entered the estuary in a consistent order over a six-week period, and estuary conditions varied widely over that time period. Therefore, populations migrating at different times of the year experience different levels of food availability and are likely to experience different levels of phenological mismatch (Fig. 5.1). Exposure to phenological mismatch also likely varies across regions as climate change is shifting the timing of spring primary productivity and peak zooplankton abundance to be earlier in some locations or more variable in others (Mackas et al., 1998, 2013; Edwards and Richardson, 2004; Allen and Wolfe, 2013; Poloczanska et al., 2013). These changes in salmon prey availability are not always accompanied by equal changes in juvenile salmon outmigration timing. For example, while regionally zooplankton peak biomass is advancing at 14 days/decade, Kovach et al. (2013) found that juvenile pink salmon (*O. gorbuscha*) in the northeastern Pacific were advancing at only 5 days/decade, and sockeye and coho (*O. kisutch*) salmon from the same watershed were not altering their outmigration phenology. Thus, risks of phenological mismatches, predicted to increase in frequency and severity under future climate warming scenarios (Kharouba et al., 2018), are influenced by both intrinsic sensitivity as well as exposure that vary within and across watersheds.

Several studies have examined survival or population dynamics as a result of phenological mismatch (Scheuerell et al., 2009; Chittenden et al., 2010; Satterthwaite et al., 2014), but few have examined mitigating traits, such as condition factor, which could alter the strength of the effect of phenological mismatch. For salmon, the early marine period is thought to be one of the major determining periods of recruitment. When more fish, on average, survive this period, more fish recruit to the population and the fishery (Pearcy, 1992). Ours is an important theoretical step towards understanding how factors, such as sensitivity to mismatch, could influence the relationship between phenological mismatch and survival.

Determining trait-based vulnerability to phenological mismatch among species and populations is imperative to predicting if and how species will be impacted by climate change and inform conservation efforts (Foden et al., 2013; Pearson et al., 2014; McLean et al., 2016). Indeed, identifying relationships between species- and population-level traits and sensitivity to change is one avenue that has been used to identify sentinel species and prioritise species of conservation concern (Williams et al., 2008; Butchart et al., 2010). Here we reveal that condition and energy status are traits that vary across and within populations, and that condition can inform starvation resistance and thus vulnerability to mismatch. Populations with higher predicted mean starvation resistance should be less sensitive to climate change-driven phenological mismatches. Thus, phenotypic traits can be useful in understanding how species and populations will respond to oncoming change through identifying population sensitivity to phenological mismatch.

5.6 Acknowledgements

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5.7 Supplemental methods

Additional description of the bioenergetics model used to estimate weight loss

The Wisconsin Bioenergetics Model is, at its core, an energy budget equation in which energy consumed is balanced by energy expended for metabolism (respiration, active metabolism and specific dynamic action), waste (egestion, excretion), and growth (somatic and gonad) (Deslauriers et al., 2017).

$$C = (R + A + SDA) + (F + U) + (SG + GG) \tag{5.4}$$

Consumption of prey C is balanced against metabolism (which is made up of three components; respiration (resting metabolism) R, active metabolism A, and specific dynamic action (energy required for energy assimilation and use, modelled as a proportion of consumption; SDA), waste (which is made up of egestion (fecal waste) F and excretion (nitrogenous waste) U) and growth (which is made up of somatic SG and gonad GG growth). Energy is allocated in the order of the equation with metabolism and waste first, with any remaining energy being allocated to growth. Each process (metabolism, waste, and growth) is determined by temperature and body size. Therefore each process and sub-process is described by a set of temperature and mass-specific functions with parameters developed for various species during controlled laboratory conditions (Tyler and Bolduc, 2008).

The equations are associated parameters that are species- and life-stage specific. We used the equations for juvenile rainbow trout, as no other juvenile salmon species was available (Tyler and Bolduc, 2008). We assumed 0 g of food was consumed (i.e., food deprivation), which represents an extreme condition. In general, bioenergetic equations for the Wisconsin Bioenergetics Model were created using experiments in which fish were fed. During starvation, metabolic processes change, and thus the metabolic equations developed for feeding fish may be inaccurate for starving fish (McCue, 2010). However, equations for fed fish represent the closest approximation that is available.

By setting consumption to zero, the Wisconsin Bioenergetics Model is simplified as excretion, egestion, and specific dynamic action are assumed to be 0. Additionally, juvenile salmon are not yet investing in gonadal growth so that term can also be set to 0. Resulting in a simplified equation:

$$0 = (R + A) + (SG) \tag{5.5}$$

$$-SG = (R + A) \tag{5.6}$$

Thus, respiration (in g O_2/g fish/d; oxy-caloric coefficient 13,560 J/g O_2), and active metabolism will result in energy loss (negative somatic growth). The rate of energy loss will be temperature and size dependent.

$$R = RA * W^{RB} * F(T) * ACTIVITY \tag{5.7}$$

Where RA and RB are the intercept (specific mass of oxygen (g O_2/g/d) consumed by a 1-gram fish at 0°C) and slope for the allometric mass function, and W is the mass of the fish. Water temperature $F(T)$ is described by the function:

$$F(T) = e^{(RQ*T)} \tag{5.8}$$

Where RQ approximates the $Q10$ (the rate at which the function increases over relatively low water temperatures) and T is temperature.

Active metabolic rate, $ACTIVITY$ in Equation 5.7 for salmon is described by the function:

$$ACTIVITY = e^{(RTO*VEL)} \tag{5.9}$$

$$VEL = ACT * W^{RK4} * e^{(BACT*T)} \tag{5.10}$$

Where RTO is the coefficient for swimming speed dependence of metabolism (s/cm), $RK4$ is the mass dependence coefficient for swimming speed at all water temperatures, and $BACT$ is the water temperature dependence coefficient of swimming speed. If swimming speed is a constant then $RK4$ and $BACT$ are set to 0, and ACT is set to the desired velocity (cm/s) (Deslauriers et al., 2017).

We ran the Wisconsin Bioenergetics Model using R statistical computing environment (v 3.6.3) (R Core Team 2020) using RStudio GUI (v 1.2.5033, 2019) and Fish Bioenergetics 4.0 (Deslauriers et al., 2017). Fish Bioenergetics 4.0 uses parameters from juvenile rainbow trout (Tyler and Bolduc, 2008) to estimate daily energy difference and estimates daily weight. Since we set the model to 0 g consumption, we observed daily weight that decreased through time. We compared predicted weight loss by the Wisconsin Bioenergetics Model to observed weekly weight loss for sockeye salmon held without food (Fig. 5.7). In general, the Wisconsin Bioenergetics Model over-estimated weight loss, especially for weeks 4 – 7, compared to observed weight changes of fish held in the lab. Over estimated weight loss

could be due to the model's assumption of average activity, ascribed to ACT. Fish held in the laboratory experiment did not move much, and so used less energy than predicted (Simpkins et al., 2003). However, in 'natural' environments fish would be expected to move, such that the observed weight loss might be less than expected in the 'natural' environment. The predicted weights were much lower than observed during weeks 4 – 7, possibly due to unaccounted for changes in metabolism due to starvation (McCue, 2010). The Wisconsin Bioenergetics Model was parameterized for feeding fish, with likely higher metabolic rates than starving fish. Therefore, it is likely that the predicted weight loss is over-estimated and thus starvation resistance estimates may be underestimated/conservative.

5.7.1 Supplemental tables

Table 5.3: P values for Bonferroni post hoc pairwise comparisons of **fork lengths (mm)** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	0.0066	**<0.0001**					
Kalum	0.33	**<0.0001**	0.84				
McDonnell	1.0	1.0	0.26	1.0			
Nanika	1.0	1.0	0.02	1.0	1.0		
Salix/Bear	**0.0013**	**<0.0001**	**<0.0001**	**<0.0001**	0.024	**0.00019**	
Sustut	1.0	1.0	**0.00081**	0.020	1.0	1.0	**<0.0001**

Table 5.4: P values for Bonferroni post hoc pairwise comparisons of **weight (g)** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	0.043	0.0038					
Kalum	1.0	0.018	1.0				
McDonnell	1.0	1.0	1.0	1.0			
Nanika	1.0	1.0	0.12	1.0	1.0		
Salix/Bear	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	
Sustut	1.0	1.0	**0.0058**	0.099	1.0	1.0	**<0.0001**

Table 5.5: P values for Bonferroni post hoc pairwise comparisons of **lipid content (%)** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	1.0	1.0					
Kalum	1.0	0.56	1.0				
McDonnell	1.0	1.0	1.0	1.0			
Nanika	1.0	1.0	1.0	1.0	1.0		
Salix/Bear	0.031	**0.0002**	0.056	**<0.0001**	0.25	0.37	
Sustut	0.92	0.13	0.92	**0.004**	1.0	1.0	1.0

Table 5.6: P values for Bonferroni post hoc pairwise comparisons of **water content (%)** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	1.0	1.0					
Kalum	1.0	1.0	1.0				
McDonnell	1.0	1.0	1.0	1.0			
Nanika	1.0	0.42	1.0	1.0	1.0		
Salix/Bear	1.0	**<0.0001**	0.11	**0.00063**	1.0	1.0	
Sustut	1.0	**<0.0001**	0.59	0.014	1.0	1.0	1.0

Table 5.7: P values for Bonferroni post hoc pairwise comparisons of **protein content (%)** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	0.022						
Johnston	1.0	1.0					
Kalum	1.0	0.090	1.0				
McDonnell	1.0	1.0	1.0	1.0			
Nanika	1.0	0.35	1.0	1.0	1.0		
Salix/Bear	1.0	**<0.0001**	1.0	0.97	1.0	1.0	
Sustut	1.0	**<0.0001**	1.0	1.0	1.0	1.0	1.0

Table 5.8: P values for Bonferroni post hoc pairwise comparisons of **energy density (MJ/kg)** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	1.0	1.0					
Kalum	1.0	1.0	1.0				
McDonnell	1.0	1.0	1.0	1.0			
Nanika	1.0	1.0	1.0	1.0	1.0		
Salix/Bear	0.077	**<0.0001**	0.11	**<0.0001**	0.19	0.22	
Sustut	1.0	**<0.0001**	0.31	**0.0022**	1.0	1.0	1.0

Table 5.9: P values for Bonferroni post hoc pairwise comparisons of **Fulton's condition factor** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	1.0	1.0					
Kalum	1.0	**<0.0001**	0.018				
McDonnell	1.0	1.0	1.0	**0.0058**			
Nanika	1.0	0.19	0.33	1.0	0.089		
Salix/Bear	1.0	**<0.0001**	0.0061	1.0	**0.0021**	1.0	
Sustut	1.0	**<0.0001**	0.053	1.0	0.016	1.0	1.0

Table 5.10: P values for Bonferroni post hoc pairwise comparisons of **starvation resistance** of populations of sockeye salmon smolts captured in the Skeena River **estuary**, α=0.00625. Significance is indicated by bold letters.

	Alastair	Babine	Johnston	Kalum	McDonnell	Nanika	Salix/Bear
Babine	1.0						
Johnston	1.0	1.0					
Kalum	1.0	**0.0019**	0.9				
McDonnell	0.56	1.0	1.0	0.33			
Nanika	1.0	1.0	1.0	1.0	1.0		
Salix/Bear	1.0	0.058	1.0	1.0	0.65	1.0	
Sustut	1.0	0.038	1.0	1.0	0.76	1.0	1.0

5.7.2 Supplemental figures

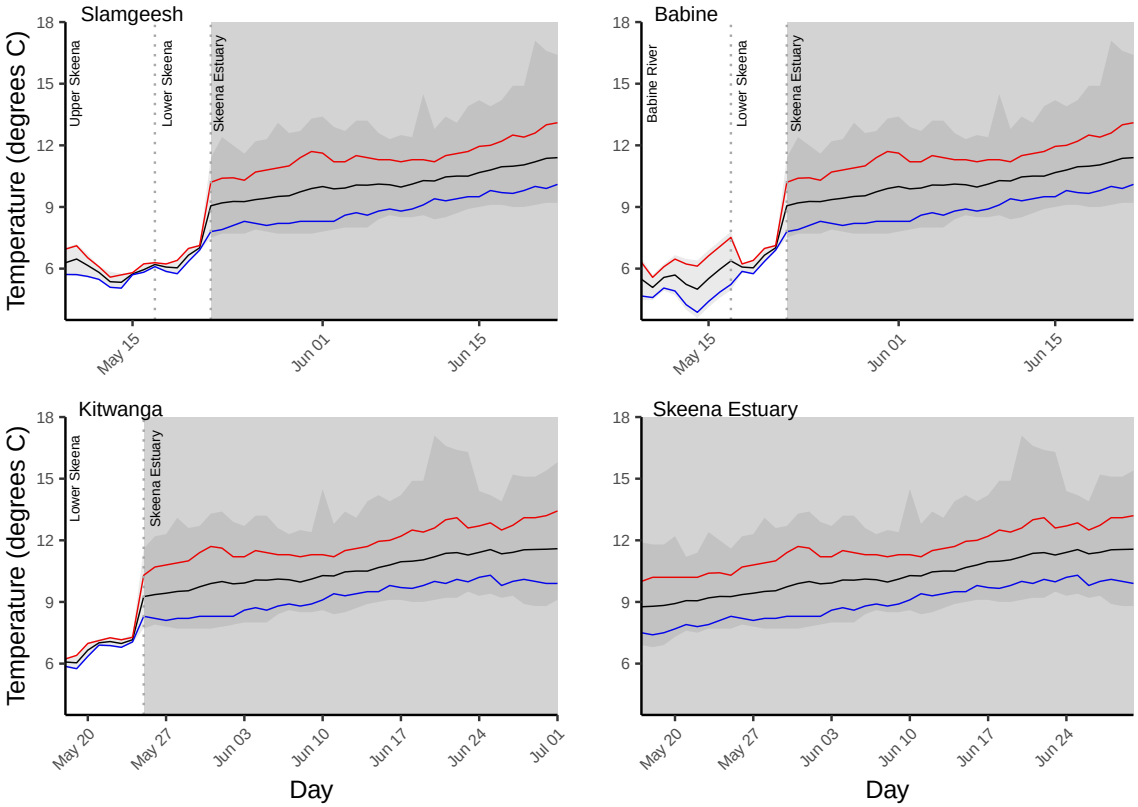

Figure 5.6: Temperature profiles used to predict weight loss for fish captured at the Slamgeesh fish fence (top left), Babine fish fence (top right), Kitwanga fish fence (bottom left), and in the Skeena River estuary (bottom right). Lines indicate 50% (black) 90% (red) and 10% (blue) data quantiles. Dark shaded region indicates range of temperature data observed. Light shaded region indicates anticipated presence in estuary or near shore coastal marine waters, vertical lines indicate migration milestones.

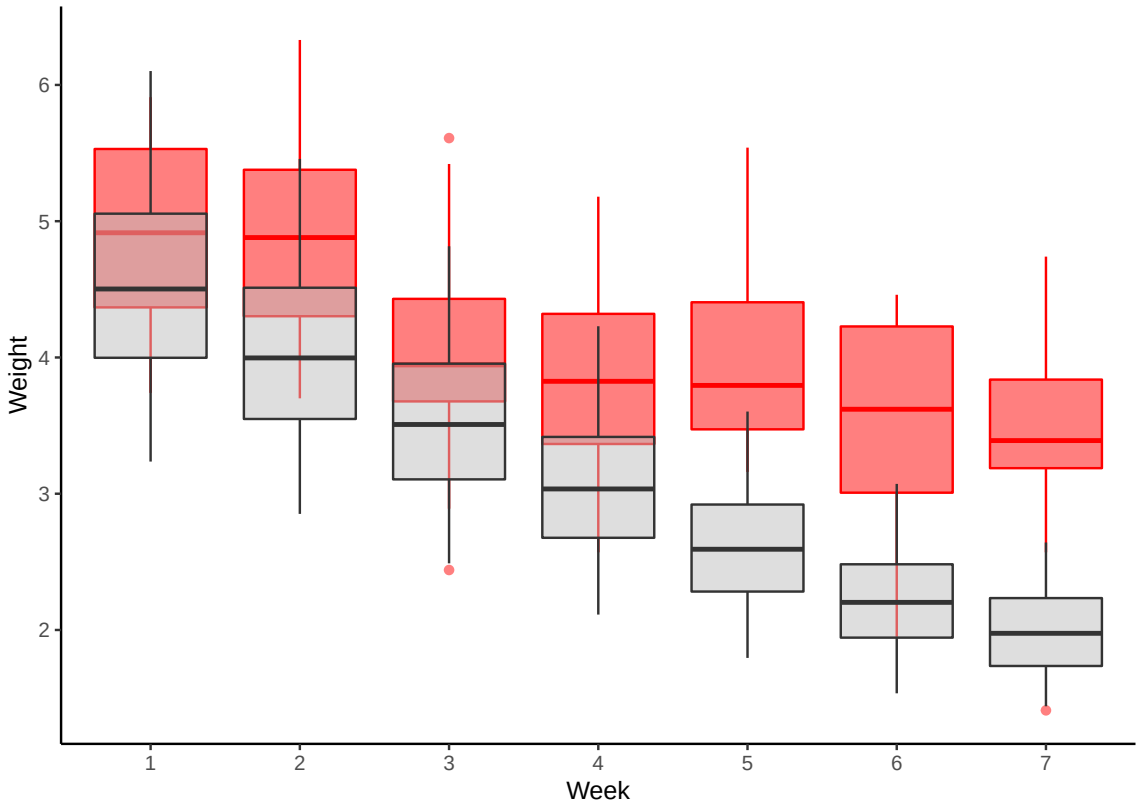

Figure 5.7: Weight of experimentally held and food deprived Chilko Lake sockeye salmon smolts (red) compared to modelled weight loss of Chilko Lake salmon smolts (black). Modelled weights used the Wisconsin Bioenergetics Model for juvenile rainbow trout, zero consumption, initial weights of sockeye salmon before food deprivation, and temperatures from the controlled experiment. Though predicted weights are consistently lower than observed, experimentally held fish did not move, and thus observed weight loss was expected to be lower than in 'natural' conditions. After three weeks observed weight loss vs. predicted weight loss begin to differ more substantially, possibly due to metabolic changes from starvation that the Wisconsin Bioenergetics Model does not account for. Boxplots show the 25^{th}, median, and 75^{th} percentiles.

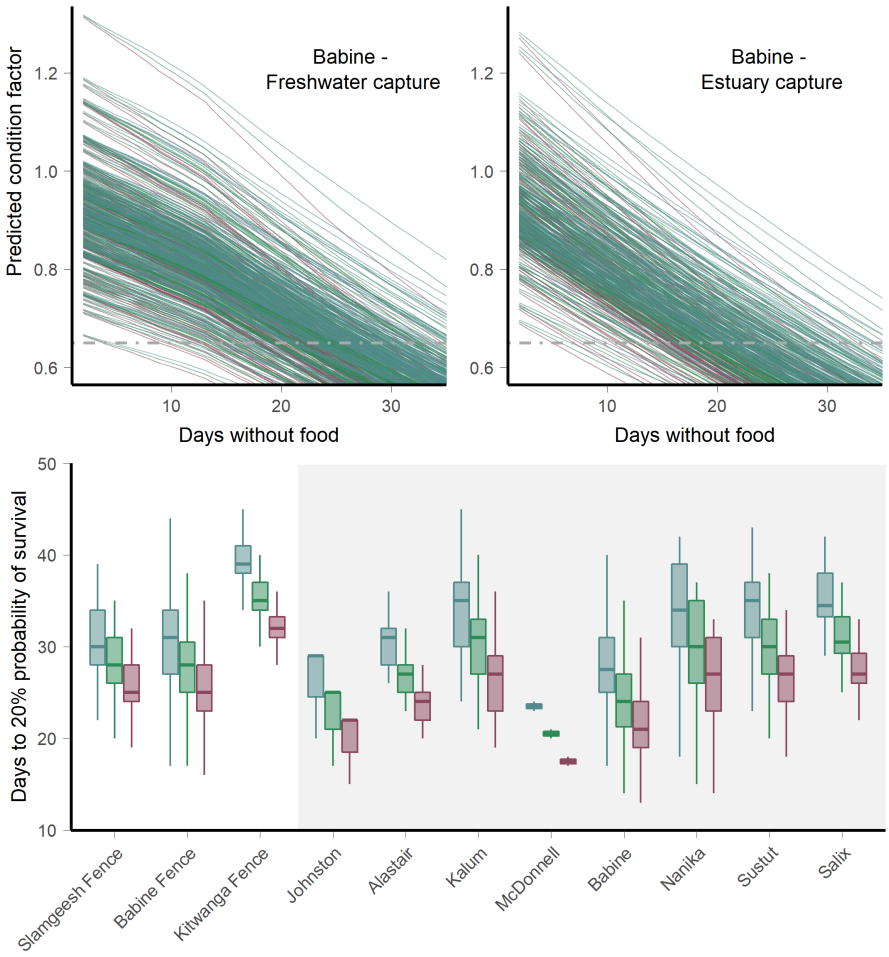

Figure 5.8: Top – Predictions of condition factor based on predicted weights from Wisconsin Bioenergetics Model output for fish captured at fence sites (left) and in the estuary (right), for three different temperature scenarios (90%, 50% and 10% quantiles of historic temperatures). Bottom - Number of days to 30% probability of survival using swim performance model, for fish captured at fence sites or in the estuary and three different temperature scenarios. Red indicates predictions with 90% quantile temperatures, green indicates predictions with median temperature, blue indicates predictions with 10% quantile temperatures. Grey shaded region represents estuary residence. Boxplots show the 25^{th}, median, and 75^{th} percentiles.

Chapter 6

General Discussion

Shifts in phenology have been some of the most well-documented and pervasive ecological effects of climate change. Yet, in the over 20 years since they were first identified as a global phenomenon, some of the simplest questions remain unanswered: Which species or populations have experienced phenological shifts? Which have experienced phenological mismatches? What impact will phenological mismatches have on species or population dynamics? In this thesis, I demonstrate that salmon populations are changing their outmigration phenologies in unpredictable ways that do not correspond to changes in the timing of spring primary productivity (Chapter 2); that across-year, but not within-year, phenological mismatches impact steelhead trout survival (Chapter 3); and that body condition can be used as a proxy for sensitivity to starvation to identify populations most sensitive to phenological mismatch (Chapters 4 and 5). Together I show that, for now, Pacific salmon (*Oncorhynchus* spp.) are likely resilient to moderate phenological mismatches. However, simultaneous changes in freshwater habitat and the marine environment may threaten this resilience.

6.1 Vulnerability to phenological mismatches

Vulnerability to phenological mismatches is determined by both exposure and sensitivity to phenological mismatches (Williams et al., 2008). Here, exposure to phenological mismatches refers to the duration and frequency of exposure to phenological mismatches between juvenile salmon and their prey, and sensitivity refers to the innate conditions which influence the severity of the impact that phenological mismatches have on salmon species or populations. This thesis tackles exposure to phenological mismatches in Chapters 2 and 3, and sensitivity to conditions associated with phenological mismatches in Chapters 4 and 5.

Salmon are not tracking shifts in the timing of spring primary productivity, potentially leading to increased frequency of phenological mismatches in the future. In both Chapters 2 and 3, salmon outmigration timing varied independently from shifts in indices of prey phenology (phytoplankton bloom timing and biological spring transition date, respectively). In

Chapter 2, salmon outmigration phenology was not correlated with shifts in annual spring phytoplankton bloom phenology. In Chapter 3, Wind River steelhead trout (*O. mykiss*) did not shift their outmigration phenology over the 14-year period, though the biological spring transition date varied annually by over 150 days. As a result, phenological mismatches occurred in some years and not others, driven by oceanographic conditions such as regional water temperature and Pacific Decadal Oscillation, which determine timing of spring phytoplankton blooms and zooplankton community composition (Peterson and Schwing, 2003; Keister et al., 2011; Fisher et al., 2015). Concerningly, in some areas, climate change is predicted to increase the variability of phytoplankton and zooplankton phenology (Allen and Wolfe, 2013), which could lead to increased frequencies in phenological mismatches between salmon and their prey that could decrease marine survival. In other regions, climate change is shifting phytoplankton and zooplankton phenology to be earlier (Edwards and Richardson, 2004; Richardson, 2008; Poloczanska et al., 2013), which could be beneficial to salmon by increasing the likelihood of phenological matches (as in Chapter 3), but only if they are followed by an abundance of energy-dense salmon prey. In fact, warmer oceans, while advancing phytoplankton blooms, often have longer food chains, with less energy-dense species, resulting in an ocean environment that is less favourable to salmon growth and survival (Peterson et al., 2014). Current environmental conditions result in periodic phenological mismatches but future climate-driven changes in salmon outmigration phenology and salmon prey phenology will likely lead to increasing exposure to phenological mismatches.

Innate traits such as body condition could determine how salmon are impacted by phenological mismatches. In Chapter 5, individuals and populations were found to have different physical and energetic condition, which translated to differences in sensitivity to starvation associated with phenological mismatch. Average starvation resistance (i.e., days to starvation) was a few weeks, demonstrating that salmon are likely resilient to some measure of mismatch. However, this was a theoretical approach to examining sensitivity to phenological mismatch and a more applied future analysis is critical to truly understanding sensitivity to phenological mismatches. For example, an interesting extension of this research would be to determine the factors that set body condition of wild salmon smolts (e.g., freshwater prey abundance, density dependence, competition) and if manipulation of these factors could change body condition and subsequent marine survival. Traits such as body condition, growth rate, and aerobic scope, likely also impact sensitivity to phenological mismatch and are all interesting avenues for further research (McLean et al., 2016). Understanding which species or populations are more vulnerable to phenological mismatch could help prioritise species/populations for conservation efforts.

6.2 Predictability of phenological change

Population-specific response diversity and local adaptations may result in diverse outcomes for a single disturbance type (e.g., climate change) that can reduce variability in abundance of species and meta-populations but can complicate management approaches (Elmqvist et al., 2003; Moore et al., 2010). I revealed within and among species diversity in shifts in Pacific salmon spring outmigration phenology that remain largely unpredictable. Consistent with previous regional studies, Pacific salmon smolt outmigration phenology is shifting differently across species, with species that spend the shortest time in freshwater, pink (*O. gorbuscha*) and chum (*O. keta*) salmon, having larger shifts than species that rear for longer periods in freshwater (Kovach et al., 2013). However, I have also demonstrated substantial within-species diversity that is not explained by environmental or geographic patterns. Indeed, other than species, no variable tested clearly explained the variability in shifts in outmigration phenology across populations, possibly due to the spatial scale of the variables being tested. Local adaptations could make Pacific salmon populations differentially sensitive to climate change, resulting in variable shifts in outmigration phenology (Crozier et al., 2008). Future research could examine potential drivers of shifts in outmigration phenology at a finer scale (e.g., watershed or tributary), but the drivers of shifts in outmigration of one population may not be representative of other populations. This response diversity could buffer a species or metapopulation from swings in population dynamics but could make predicting how a single population will respond to a phenological mismatch impractical. Therefore, a predict-and-prescribe approach for species conservation and management may not be effective for species with highly locally adapted populations that are part of metapopulations making use of diverse habitats across a broader area (Schindler and Hilborn, 2015). Rather than focussing on predicting when phenological change and subsequent mismatches will occur, I suggest employing precautionary approaches which conserve the habitat and biodiversity that make salmon resilient to climate change.

6.3 Marine survival and phenological mismatches

Conditions during the freshwater migration and early marine life stage can elicit broad population-level patterns in marine survival. There is mounting evidence that phenological mismatches during the early marine life stage of Pacific salmon can impact marine survival and adult recruitment into the fishery (Chittenden et al., 2010; Satterthwaite et al., 2014; Malick et al., 2015a). Faster growing, larger smolts are more likely to survive the marine environment (MacFarlane, 2010; Fiechter et al., 2015), such that when preferred prey are abundant at the time salmon arrive in the estuary, marine survival is higher (Chittenden et al., 2010; Satterthwaite et al., 2014; Malick et al., 2015a). However, phenological mismatches are not the only factor that may impact the marine survival of salmon species. Indeed, in Chapter 3 the annual outmigration date at which marine survival was optimised

shifted across years independently of the timing of peak northern zooplankton availability. This suggests that other intra-annual factors (e.g., flow rates; Perry et al. 2018) either during the freshwater migration or in the marine environment impacted survival. Larger temporal scale oceanographic patterns such as Pacific Decadal Oscillation, as well as variation in regional oceanographic variables such as water temperature and upwelling strength, can impact marine survival of salmon through bottom-up processes (Nickelson, 1986; Mantua et al., 1997; Mueter et al., 2002b,a); though these relationships may change through time (Rupp et al., 2012). Furthermore, predation pressure and inter- and intra-specific competition can also impact marine survival (Ruggerone et al., 2003; Hostetter et al., 2015; Nelson et al., 2019). Thus, phenological mismatches are part of a larger mosaic of conditions that impact marine survival and may be changing due to anthropogenic disturbances such as climate change.

6.4 Carryover and cumulative effects in salmon

Marine survival is not determined solely by marine conditions but can be influenced by conditions salmon experience during freshwater rearing. For example, freshwater conditions such as inter-specific competition, density dependence, predation, and water temperature can determine size at outmigration (Schindler et al., 2005; Rich et al., 2009; Bailey et al., 2018), and size is an important predictor of marine survival, with larger fish having higher survival than smaller fish (Healey, 1982; Ward et al., 1989; Henderson and Cass, 1991; Duffy and Beauchamp, 2011). In fact, size at outmigration was the best predictor of marine survival in steelhead trout smolts in Chapter 3, regardless of ocean growing conditions or phenological mismatches. Thus, changes to the freshwater environment that alter fish growth and body size can subsequently impact ocean survival. Freshwater salmon habitats have been degraded and disconnected through activities such as logging, water withdrawal, and habitat destruction (McClure et al., 2008). Changes to freshwater habitat could have carryover effects with surprising impacts on marine survival through altering smolt size, size-at-age, and condition, as well as outmigration timing.

The impact of phenological mismatches may be modulated by individual smolt body condition such that changes in freshwater habitat that decrease smolt condition could have cumulative effects that decrease marine survival. Chapter 5 showed that starvation resistance, a proxy for sensitivity to a phenological mismatch, differed within and among populations. Individuals and populations with lower body condition and thus lower starvation resistance, may be more vulnerable to phenological mismatches (Saloniemi et al., 2004). Therefore, the impact of phenological mismatches may be filtered through carryover effects from freshwater. If this is the case, the effects of changes in body condition may be masked by good ocean growing conditions. Consequently, impacts of decisions which affect smolt body condition may not be immediately observed, instead becoming apparent in years with

poor ocean growing conditions such as during a phenological mismatch. Interestingly, when I examined the interaction between size and survival across years in Chapter 3 this term was not included in the final model set. It is possible that steelhead are less sensitive to phenological mismatches because of their large size at outmigration, or that there were not enough years with phenological mismatches to have the statistical power to detect the effect of the interaction. Future research should examine how body condition impacts survival across multiple years with and without phenological mismatches to determine if there could be cumulative effects between freshwater disturbance and phenological mismatches. Importantly, climate warming is resulting in higher variability in the timing of marine primary productivity (Allen and Wolfe, 2013; Edwards and Richardson, 2004; Richardson, 2008), which may increase the frequency of phenological mismatches. Simultaneous changes to freshwater habitat and increased phenological mismatches could have carryover and cumulative effects that impact marine survival and population dynamics of salmon.

6.5 Final thoughts

Pacific salmon exemplify the challenges facing migratory animals due to overwhelming anthropogenic disturbance, including habitat destruction and climate change. Long distance migrations can be challenging periods with higher-than-average mortality and can be key periods for shaping population abundance (Sillett and Holmes, 2002; Klaassen et al., 2014; Clark et al., 2016; Lok et al., 2015). Survival often depends upon conditions faced before, during, and after migration (Alerstam et al., 2003; Drent et al., 2003), such that phenological mismatches with prey are one part of a larger mosaic of interactions and conditions that can determine survival. For example, non-random destruction of freshwater habitat could reduce both the phenological diversity of populations (McClure et al., 2008) as well as individual body condition, possibly increasing the magnitude of exposure and sensitivity to phenological mismatches in Pacific salmon. Simultaneously, climate change is warming the oceans resulting in shifts in prey timing and decreases in prey nutritional content, making the marine environment less favourable to the growth and survival of salmon, particularly in the southern extent of their range (Peterson et al., 2014; Fisher et al., 2015). These human activities span the salmon life-cycle and could have cumulative effects which may erode the resilience of Pacific salmon to future phenological mismatches. Likewise, other migratory species face carryover and cumulative effects that can impact survival in complex and sometimes surprising ways.

Conserving migratory species requires an integrative understanding of many key traits including morphological, physiological, behavioural, and life-history traits (Bowlin et al., 2010). In this thesis, I have used a broad range of approaches ranging from data syntheses to targeted experiments to interrogate how broad patterns and mechanistic underpinnings can contribute to the outcomes of phenological mismatches. I have shown that size and

condition at outmigration, and outmigration timing are key traits which can impact marine survival of salmon. I have also shown the challenges associated with studying complex migratory animals whose life spans multiple habitats. In fact, while Pacific salmon are some of the best studied migratory animals in the world, we still lack the data to predict why phenology is shifting across populations. Can we ever know enough to predict future responses to anthropogenic or climate change? Perhaps, rather than predicting responses to climate change or anthropogenic activities, we should apply a precautionary approach and aim to understand and conserve the biodiversity and habitat that supports species' resilience.

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